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Aggression-affiliation Motifs in Bottlenose Dolphins' Social Networks

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Abstract

Networks in biology have provided a powerful tool to describe and study very complex biological processes and systems. In this master thesis, we are interested in a specific type of biological system: social groups of animals. Social network analysis allows us to study many different processes that take place in animal social groups ranging from the formation of hierarchies and alliances within group members to the transmission of information. Furthermore, using network analysis we can explore the emergence of different patterns of behaviour at the group and population level. In this work, we focus on how conflict dynamics and postconflict interactions shape social networks of groups of captive bottlenose dolphins. Examining changes to the social structure over time can broaden our understanding of the functions, dynamics and organization of animal social groups. With this aim in mind, we first examined temporal changes and aggression-affiliation motifs in the observed bottlenose dolphins' network structure. Then, using the results of the previous analysis we built two models that simulate the dynamics of aggression and affiliation in a small group of dolphins. This type of models can help us to broaden our understanding on the factors influencing the social dynamics of dolphin groups.

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1 Introduction

1.1 Complex Networks in Biology

The broad field of 'complex systems' has experienced great advances in the past two decades. Due to the lack of consensus on the formal definition of 'complexity' within the scientific community, complex systems are usually characterized by some common properties. One of the most popular characterizations of complex systems is the one that depicts them as systems composed by many components that interact with each other [1]. Therefore, behind a complex system there is a complex network that contains the components and the interactions between the different elements of the system [2]. One crucial feature of these systems is that their properties arise from the interactions. Thus, these systems cannot be understood only considering their individual components since the whole is more than the sum of its parts [3]. In complexity science this concept is called emergence. In this way, this type of systems has the potential of displaying novel properties or behaviors that might differ from the ones displayed by its individual components in isolation. There are many different systems that meet these criteria. For example, systems such as the internet, social networks, ecosystems or the brain are constituted by multiple components that interact with each other and display emergent properties. For this reason, the study of complexity is a broad interdisciplinary field that can be applied to many areas of research like physics, sociology or biology.

Interestingly, one of the pioneers in conceiving biological systems as interconnected complex networks was a German naturalist and explorer, Alexander von Humboldt. At the beginning of the XIX century, he already described nature as a web of life in which everything was linked: "In this great chain of causes and effects, no single fact can be considered in isolation" [4]. That is, Humboldt looked at the bigger

picture unlike the vast majority of the naturalists of his time that were focused on collecting and classifying nature in smaller taxonomic units. His pioneer idea was to understand the natural world as a dynamic web of entwined parts, this conception was one of the foundational principles of modern ecology. Humboldt ideas implied that the reductionist approach to nature was limited and, as complexity science does nowadays, defended that one cannot fully describe the properties of a system at a given scale in terms of the features at a lower scale [3]. This idea brings us back to one of the key concepts in complexity theory: emergence. Humboldt, instead of focusing on the differences between natural processes or organisms to describe them, tried to find similarities and global patterns. Currently, this is a common practice in complexity and network science: the search for common patterns and statistical properties across apparently different systems [5]. This approach is very useful since it allows us to find similar mechanisms and architectural constraints that appear in different types of systems [5].

The network approach in biology has provided a powerful tool to describe and study very complex communities and processes. This field and its methodology can be applied to different biological processes ranging from genetics to evolution. Biological systems can be described as complex systems formed by multiple parts in interaction.This structure can be observed in multiple levels of biological organization, starting from genes and their networks of genetic interactions, and cells and their complex metabolic pathways. At the tissue and organ level we can also observe complex systems such as the brain, which is composed by millions of neurons that interact with up to thousands of others. Individuals and their interactions with others and their environment also form networks like food webs composed by paths of energy and nutrients through the living beings of an ecosystem. Finally, even evolution can be devised as an intricate network of feedbacks in which individuals drive environmental changes, and in turn these altered environments select for changes in

individuals [6]. Thus, the perspective of complex systems help us to understand how certain real-world systems are structured, their dynamics and the existing interactions between them.

In this master thesis we are interested in a specific type of biological system: social groups of animals. In the following section we will describe more deeply the features and principal characteristics of this particular biological complex system.

1.2 Animal Social Networks

Living in groups provides many survival benefits to social animals. Some of those benefits are protection, mate choice, aid in the rearing of young, reduction of the risk of predation, increased reproductive fitness or higher probabilities to find resources [7, 8]. Therefore, for group-living species, it is crucial to maintain social relationships within the group. Positive (affiliative) and negative (agonistic) interactions between group members are key for establishing and maintaining those relationships. Furthermore, these in-group interactions shape the hierarchy and social structure of the species.

Affiliative interactions such as grooming not only serve to strengthen and maintain social bonds but also to foster social tolerance, decrease aggression, and increase cooperation and assistance between group members. Furthermore, affiliative contacts can be exchanged for social goods and services [9].

Aggressive interactions are also common in social groups. For example, conflicts of interest over access to mating partners, resources or positions in the dominance hierarchy may result in aggressive encounters within group members. Conflicts are costly in terms of energy, risk of injury and disruption of social relationships between group members [10, 11, 12]. Thus, in species that rely on cooperation and mutual assistance for their survival, the occurrence of aggression might be constrained by the

need to maintain the group's social relationships [10, 13]. Therefore, the reproductive and survival success of both opponents may depend on how conflicts are stopped [14] and resolved [15]. Social species are then expected to develop ways to control and palliate the consequences of in-group aggression [10, 13]. In fact, post-conflict management mechanisms are widespread among different social species of primates, canids, or birds [12, 16, 17, 18, 19]. Active conflict resolution could mitigate the cost of conflicts and prevent further aggression by means of affiliative interactions that take place after an aggressive encounter [11]. After the end of the aggressive event thus former opponents may display a variety of interactions that may alleviate post-conflict distress, reduce aggressive tendencies in both parties, or restore relationships between former opponents [11]. Some of those post-conflict interactions are reconciliation (affiliative post-conflict contacts between former combatants), third-party affiliation (affiliative post-conflict contacts between one of the rivals and a bystander) or redirected aggression (post-conflict aggressions directed to a bystander by one of the former opponents) [17, 20].

Individual social interactions between group members can have a strong influence on group function and structure [21]. Therefore, the social network approach provides a powerful tool to study and understand the form and function of social relationships in animal groups. In fact, recently there has been great interest in animal social networks within the field of behavioral ecology. These networks are constituted by nodes representing the members of the group connected through a set of links which represent the different interactions between them. Links can be characterized by a binary variable (e.g. 0 or 1 indicating respectively the existence or not of an interaction), this type of networks are called unweighted [22]. Links can also be characterized by a number indicating the weight of the interaction and, in this case, the network is called weighted [22]. Moreover, in animal social networks we can also find signed networks in which the interactions between group members are described

by a sign (+ or -) indicating positive (affiliative) or negative (aggressive) interactions respectively.

Social network analysis allows us to study many different processes that take place in animal social groups ranging from the formation of hierarchies and alliances within the members of the group, to the social transmission of information. This approach provides a way to study animal behaviour in the context of the animal's social environment. Moreover, using the network analysis we can explore the emergence of patterns of behaviour at the group and population level [21]. Thus, the network approach can serve to understand how the individual traits are linked to group or population level processes [21].

In this work, we are interested in how conflict and conflict resolution shape social networks in time. Several studies have assessed the impact of social conflict in network structure in different social species. For example, Dey and collaborators [21] used the social network approach to study spatial associations and patterns of dominance interactions in captive social groups of a cooperatively breeding fish (*Neolamprologus pulcher*). Many other studies have assessed how affiliative networks are structured and their impact on different individual traits such as reproductive success or survival [23, 24, 25, 26, 27].

There are many methodological advancements in social network analysis that can be applied to the study of animal sociality. On the one hand, focusing on the structure and function of certain network motifs has been a common way of studying social processes since these local interactions may link behaviours at the individual level with emergent network patterns [27]. Networks motifs are defined as "patterns of interconnections occurring in complex networks at numbers that are significantly higher than those in randomized networks" [28]. Examining aggressive and affiliative motifs in social networks can shed light on the mechanisms underlying the structure of the network. On the other hand, an underutilized approach to animal sociality is

the examination of temporal changes in social networks [29]. Aggressive and affiliative interactions among individuals of a social group are dynamic processes, however most of the works on animal social networks assess static structures [29]. Animals might change their social interactions according to the result of previous contacts with the same or other individuals. For example, a highly aggressive encounter between two group members could modify the whole structure and dynamics of the social network of the group. Furthermore, these social interactions may change in response to variations of the external conditions (e.g. climate, predation...) [29]. Therefore, it is crucial to take into account the temporal dynamics that influence animal social networks to better identify and understand the factors affecting animal sociality and the functions of social organization [29].

1.3 Bottlenose dolphin, animal model for the study of social networks

Bottlenose dolphins *(Tursiops truncatus)*, are ideal candidates for the study of the dynamics of affiliative and aggressive interactions in social networks since they are a highly social species. Wild bottlenose dolphins live in fission-fusion societies that are characterized by frequent variations in the composition of the group, flexible dominance relationships, and high levels of cooperation [30]. Despite the dynamical changes of the composition of the group, dolphins are dependent on their social partners establishing complex and stable relations with some group members [13].

In bottlenose dolphins' groups the most stable associations are among same-sex members, and between mother and calf pairs [31]. Some male dolphins form strong and long-lasting bonds with other males, whereas others are solitary [32, 33]. Furthermore, males often form alliances with two or three individuals, and several of these alliances can cooperate forming multiple-level alliances to herd and control females

and/or attack other alliances [32, 33]. On the other hand, females display a large variability in their association patterns establishing less stable bonds than males [34]. Some females have long-term relationships with specific individuals and, at the other end, other females are solitary or have few or no valuable partners [31, 34]. Finally, associations between females and males are generally weak and related to females' reproductive state [31, 34].

Lusseau [35] described the social structure and associations of a community of wild bottlenose dolphins using the social network approach (see Figure 1).

Figure 1: Dolphin small-world network. Image extracted from [35].

His results showed that not all dolphins have an equal role in the group. There were few individuals that represented "centres" of associations (hubs). That is, these dolphins had many associations with other members of the group and were old individuals especially females. Therefore, the dolphin network was characterized by the presence of individuals with many associations and individuals with just a few, features that matched the pattern of associations observed in bottlenose dolphins'

societies.

On the other hand, like other species sharing a similar social structure, conflicts are common among bottlenose dolphins [36]. Thus, they are expected to display active conflict resolution which allow them to develop and maintain long-lasting complex social bonds despite frequent conflict. In fact, several studies have shown that captive bottlenose dolphins display post-conflict mechanisms such as reconciliation and third-party affiliation [13, 30, 37, 38]. For example, Yamamoto and collaborators [37] showed that both winners and losers initiate reconciliation soon after the end of a conflict. Furthermore, these affiliative interactions decreased the probability of renewed aggression between former opponents and were more frequent between individuals sharing a strong affiliative bond [37]. In addition, two studies reported the occurrence of third-party affiliation in different groups of captive bottlenose dolphins [37, 39]. These affiliative interactions also reduced the probability of renewed aggressions suggesting that these contacts may serve to ease tension and reduce the probability of another conflict [39].

1.4 Aims

This master thesis seeks to contribute to the study of social dynamics of dolphins using some of the tools provided by the network approach. With this general aim in mind, the following specific objectives were pursued:

1. Study the network architecture of groups of captive bottlenose dolphins using network motif analysis. Examining the most common affiliative and aggressive motifs present in these networks can help us to better understand the social dynamics of these mammals.

2. Examine how conflict and conflict resolution shape dolphins' social networks in time. Using temporal networks allows us to study whether after conflicts dolphins

engage in post-conflict resolution interactions and the importance of these contacts in the structure of the social networks. We also built two different models of affiliative and aggressive interactions to simulate the social dynamics of a small group of dolphins. One of the models includes the pattern of conflict resolution strategies recorded from a group of captive dolphins, whereas the other model does not take into account this type of contacts. Thus, the comparison between the social networks and motifs obtained in the models and the ones coming from he real data allows us to examine the influence of postconflict management mechanisms on the network structure.

2 Methods

2.1 Subjects and facility

We observed two groups of Atlantic bottlenose dolphins housed at Marineland Mallorca. One of the groups was composed by four individuals (Group 1: two adult males, and two adult females) and the other was constituted by five individuals (Group 2: two adult males, two adult females and one juvenile male). The two adult males and one of the females were the same in both groups (see Table 1).

Subject	Sex	Age (years)	Group and identification number in the network
Estel	F	13	Group 1 : 1
Mateo	M	13	Group 1 and 2 : 2
Blava	F	13	Group 1 : 3 Group 2 : 1
Blue	M	25	Group 1 and 2 : 4
Stella	F	8	Group 2 : 3
Aitamy	M	7	Group 2 : 5

Table 1: Age, sex, group and identification number in the network of the observed dolphins. M: male; F: female.

The dolphins were kept in three outdoor interconnecting pools: a main performance pool (1.6 million litres of water), a medical pool (37.8 thousand litres of water) and a small pool (636.8 thousand litres of water). During the observational periods the dolphins had free access to all the pools. Underwater viewing at the main and the small pool was available through the transparent walls around the rim of the pools.

Ethics statement

This study was approved by the UIB Committee of Research Ethics and Marineland Mallorca. This research was conducted in compliance with the standards of the European Association of Zoos and Aquaria (EAZA). All subjects tested in this study were housed in Marineland Mallorca in accordance with the Directive 1999/22/EC on the keeping of animals in zoos. This study was strictly non-invasive and did not affect the welfare of dolphins.

2.2 Behavioural observations

Data collection

Behavioural data were collected in situ by APM from May to November 2016 for Group 1 and from November 2017 to February 2018 for Group 2. In addition, all observational periods were recorded using two waterproof cameras SJCAM SJ4000. Observations were conducted at the main pool between 8:00 am and 11:00 am. Due to the schedules and dynamics of the zoo we were unable to collect data outside this period. Dolphin social behavior was registered and videotaped for 30 min - 2 h each day. Only data from sessions that lasted at least 30 min were included in the analysis. We did not collect any data during training or medical procedures and resumed the observational session few minutes after the end of these events.

We recorded all occurrences of affiliative and aggressive interactions and the identities of the involved individuals. Aggressive contacts were defined by the occurrence of chasing, biting, and hitting, as established in previous studies [30, 36, 39, 37, 38]. Affiliative contacts were defined as contact swimming, synchronous breathing and swimming (at least 30" of continuous swimming) or flipper-rubbing, as established in previous studies [30, 39, 37, 38, 40]. We also recorded the identity of the individual

initiating the affiliative or aggressive contact [37, 38]. There were some blind spots in the pools where we could not record dolphins' behaviour. Therefore, in the few cases in which we were unable to identify the individual initiating the aggressive or affiliative event we discarded the observation.

To examine the effect of valuable relationships on dolphins'social interactions, we calculated the index of affiliative relationships (IA) between the dolphins following the procedure described in Yamamoto et al. (2016) [38]. As swimming in synchrony is a well defined affiliative behaviour in dolphins, we recorded the relative frequencies of this behaviour for calculating the IA in these groups of captive bottlenose dolphins. Data of synchronous swimming between dolphins were recorded using group 0–1 sampling [41] at 3-minute intervals. This method consists in the observation of individuals during short periods of time and the recording of the occurrence (assigning to that period a 1) or non-occurrence (assigning to that period a 0) of a well defined behaviour[41]. For calculating the IA for each couple, the number of sampling periods in which synchronous swimming between individuals A and B occurred (X_{AB}) was divided by the number of sampling periods in which the individuals A and B were observed (Y_{AB}) [38, 42].

$$IA = \frac{X_{AB}}{Y_{AB}}$$

Therefore, the IA reflects the level of affiliation for each dolphin dyad based on the pattern of synchronous swimming. This index served to construct the affiliative social networks of both groups of dolphins.

2.3 Social Network Construction

We used behavioral observations to construct social networks for each group of dolphins. Each individual dolphin was treated as a node (N) with their aggressive and

affiliative interactions supplying the network links. The daily observations were divided in periods of three minutes. We assigned a positive (+1), negative (-1) or neutral (0) interaction to each pair of dolphins of the group in each time period. That is, if during the three-minute period a pair of dolphins displayed affiliative interactions we assigned a +1 to the link between that pair of nodes, if they were involved in a conflict we assigned a -1 to the link between that pair and if the pair did not engage in any affiliative or negative interaction we assigned to that link a 0. If during the same period, the pair displayed both aggressive and affiliative interactions we took into account the last observed interaction to assign a positive or negative connection to the pair. Therefore, we obtained an adjacency matrix (an N x N matrix describing the links in the network) for each group of dolphins. So, for each day we had a set of different signed networks of the group within a specific time window (a network for each three-minute period).

These temporal networks can provide insight into social events such as conflicts and post-conflict interactions in which the order of interactions and the timing is crucial. Furthermore, they allow us to calculate the probabilities of the different affiliative and aggressive interactions occurring in the group as we will describe with more detail in the following sections.

2.4 Social Network Analysis

Time-aggregated networks

We collapsed the temporal networks of each day in time-aggregated networks. This approach consists in aggregating the data collected over time within specific intervals to create weighted networks [29]. This procedure gives rise a series of static representations of the social structure of the group of dolphins. To obtain these time-aggregated networks we proceeded as follows:

First, for each day we aggregated the values of each interaction of the networks obtained for each 3-minute period until one link qualitatively changed. We considered a significant change if one interaction passed from being negative (-1) to positive (+1) meaning that the pair of dolphins reconciliated after the conflict, or if a new affiliation (+1) or aggression (-1) took place, that is the link changed from being neutral (0) to positive or negative. If a link changed from being negative or positive to being neutral, we considered that this interaction has not changed qualitatively and continued aggregating the values of the following interactions until a significant change occurred. Therefore, a conflict or an affiliation may extend over several 3-minute periods containing several negative or positive interactions or neutral contacts and will be considered finished when the interaction change its valence. So, in the text, the terms "conflict" and "affiliation" will be used according to this definition.

Finally, what we obtained was a series of time-aggregated networks for each day. These networks are characterized by the sign and the weight of the links indicating the duration of the interaction in time. For example, if the same type of interaction (e.g. affiliation) lasted in time it is reflected by the value of the weight of the interaction. Thus, this type of networks retains the information on the duration, timing and ordering of the affiliative and aggressive events in the group.

Network motifs

The study of network motifs, recurring and significant patterns of interconnections [28], can be used to characterize families of networks [43]. It has been shown that different types of networks display different motifs [43]. Therefore, this approach could serve to uncover the basic structural elements, like interaction signatures, particular to each class of networks [28]. Furthermore, these signatures may indicate differences in functionality between networks [44]. For example, it has been found that social networks usually display bidirectionally-connected cliques, which may indicate that

individuals mutually strengthen relationships with their neighbors [28].

We examined the local-scale structure of the affiliative-aggressive social networks using motif analysis. Thus, for each of the two group of dolphins, we analyzed the network motif representation of temporal and time-aggregated networks. We identified and recorded the number of occurrences of each motif in both types of networks.

2.5 Model of affiliative and aggressive interactions

We built two models (a simple and a complex one) that aim to simulate the dynamics of aggressive and affiliative interactions of a small group of dolphins. The simpler model only included the probability of aggression and affiliation between group members, whereas the complex one also included the patterns of conflict resolution previously observed. In this way, the complex model served to assess the influence of postconflict management mechanisms on the observed pattern of aggressive/affiliative networks. To implement the models, we used the data of the group of four dolphins. We used data coming only from this group since we had more hours of video recordings and, thus, more statistics of the pattern of dolphins' interactions.

Therefore, the simple model consists of a group of four dolphins that engage in positive or negative interactions with each other following the probabilities previously recorded for these type of contacts. In turn, the complex model is also composed by a group of four dolphins which interact with each other. However, this model keeps track of past actions. That is, depending on the interaction that took place on the previous step, the probability of affiliative or aggressive interaction in the next step changes based on the observed pattern of conflict resolution. Both models return affiliative/aggressive temporal networks constituted by 4 nodes and different aggressive, affiliative or neutral interactions between the six possible pairs of individuals in the network. We simulated data for 20 three-minute periods per day for a total of 80

days. We obtained one temporal network for each period, thus, in total, we had 1600 temporal networks. We ran 100 realizations of each model.

The pattern of interactions was simulated based on the observed probabilities of aggressive and affiliative contacts of this group of captive dolphins. For the simple model we calculated the probability of general aggression and affiliation per day without distinguishing between types of positive and negative interactions. Thus, we obtained the number of periods in which an aggressive or affiliative contact took place per day and divided it by the total number of periods of that day. In this way, we obtained the probability of general aggression or affiliation per 3-minute period. On the other hand, to construct the complex model, we did distinguish between types of affiliative and aggressive contacts. Therefore, we calculated the probabilities of reconciliation, new affiliations and new aggressions per day. That is, the probability that former opponents exchange affiliative contacts after an aggressive encounter (reconciliation) and the probabilities that a conflict may promote new affiliations (third-party affiliation) or conflicts (redirected aggression) between one of the opponents and a bystander in the same day. Therefore, to classify affiliations and aggressions in these categories we used the temporal networks and examined the interactions that took place after a conflict between former combatants and between the opponents and bystanders.

Probability of reconciliation: We calculated the probability of reconciliation per day (prd). We counted the number of times former opponents reconciled after each conflict and divided it by the number of conflicts that occurred that day. That is, whether a negative link between a pair of dolphins change to a positive link in the same day:

$$prd = \frac{(num\ of\ reconciliations)}{(num\ of\ conflicts\ per\ day)}$$

To calculate the total probability of reconciliation (pr) we added all the probabilities per day and divided them by the number of days in which a conflict took

place:

$$pr = \frac{\sum prd}{(num\ of\ days\ with\ conflict)}$$

Probability of new affiliation/aggression: For each day, we calculated the probability that, after a conflict, a new affiliation (pfd) /aggression (pgd) occurred between one of the former opponents and a dolphin not involved in the conflict.That is, the probability that a positive/negative link creates a new positive/negative link between one of the former combatants and another dolphin of the group. Thus, we counted how many times one of the former opponents engaged in a new affiliative or aggressive interaction with a third party for each conflict and divided it by the number of possible affiliative/aggressive interactions that could have taken place after each conflict that day. That is, in the group of four dolphins, four new affiliations/aggressions could take place (2 between each of the former opponents and the two bystanders), thus the probability of new affiliations/ aggressions per day was:

$$pfd = \frac{(num\ of\ new\ affiliations)}{(4\ x\ number\ of\ conflicts\ that\ day)}$$

$$pgd = \frac{(num\ of\ new\ aggressions)}{(4\ x\ number\ of\ conflicts\ that\ day)}$$

To calculate the total probability of new affiliations (pft) /aggressions (pgt) we added all the probabilities per day and divided them by the number of days in which a conflict took place.

$$pft = \frac{\sum pfd}{(num\ of\ days\ with\ conflict)}$$

$$pgt = \frac{\sum pgd}{(num\ of\ days\ with\ conflict)}$$

After having calculated the probabilities per day we obtained the rate (r) of reconciliation, new aggressions and new affiliations per minute using the following formula:

$$p = 1 - e^{-r\Delta t}$$

Using the same formula we calculated the probability of reconciliation (pr), new aggression(pg) and affiliation (pf) per 3-minute period.

Finally, we calculated the probability of spontaneous aggression and affiliation per day. That is, the probability that an affiliation or an aggression took place without being derived from a previous conflict. That is, the appearance of a new positive or negative link between two dolphins that have not been related with a previous conflict. If a pair of dolphins reconciled after a fight we assumed that the following affiliative or aggressive interactions occurring in the group were spontaneous and were not a consequence of that conflict.

Probability of spontaneous affiliation/aggression: First,we obtained the number of spontaneous affiliations and aggressions per day. For the affiliations, we subtracted from the total number of affiliations per day the number of reconciliations and new affiliations. For the aggressions, we subtracted the number of new aggressions to the total number of aggressions per day. Then, we divided the number of spontaneous affiliations/aggressions per day by the total number of periods of that day. Finally, to calculate the probability of spontaneous contacts per 3-minute period, we added the probabilities per day and divided them by the number of recording days.

Our model, thus, works as follows: At the beginning of the simulations, all the interactions between the four nodes are neutral (0). In each period, we select a pair of nodes randomly and we assign to that link a positive (+1) or a negative (-1) interaction with probability p (calculated previously for each type of interaction). These interactions correspond to spontaneous aggressions and affiliations. In the complex model, if in the previous period a conflict took place, we first evaluated the different possible post-conflict contacts that could occur between the former opponents and

between them and a bystander. That is, we took into account the probability of reconciliation and the probabilities that the previous conflict gives rise to new aggressions and affiliations between the former opponents and another individual in the current period. Therefore, for reconciliations, we change the valence of the interaction from negative to positive with probability pr. We also choose randomly a pair of nodes including one of the former opponents and assign to that link a positive or negative interaction with probability pf/pg to simulate the occurrence of new affiliations or aggressions arising from the previous conflict.

Lastly, we obtained the time-aggregated networks for the two models. We also carried out a network-motif analysis. As we did not take into account the identities or gender of the nodes in these models, we grouped the obtained motifs into equivalent categories taking into account the particular pattern of interactions between vertices. We also classified the motifs obtained from the real data of Group 1 into those equivalent categories. Finally, we compared the pattern of equivalent network motifs of the observed social network of dolphins and the ones of the two models. To do so we calculated the Spearman's rank correlation coefficient (r_s), defined as a nonparametric measure of the statistical dependence between the ranking of two variables:

$$r_s = \frac{cov(rg_X\, rg_Y)}{\sigma_{rg_X}\, \sigma_{rg_Y}}$$

rg_X and rg_Y are the rank variables; $cov(rg_X\ rg_Y)$ is the covariance of the rank variables, σ_{rg_X} and σ_{rg_Y} are the standard deviations of the rank variables. Therefore, this coefficient allows us to assess the statistical dependence between the motif ranking of the real data and the one of each model.

2.6 Computational implementations

We ran 100 realizations of both models. All the models, network construction and visualization and motif analysis were generated and implemented using MATLAB R2018b [45].

3 Results

A total of 217 affiliations and 133 conflicts were registered in Group 1 during the 80 days of recordings. In Group 2, a total of 91 affiliations and 44 conflicts were collected during the 23 days of recordings. Table 2 and Table 3 show respectively the number of different types of affiliations and conflicts recorded for each group.

Type of affiliation	Group 1	Group 2
Reconciliations	41	16
New affiliations	35	17
Spontaneous affiliations	141	58
Total number of affiliations	217	91

Table 2: Total number of the different types of affiliations registered in both groups of dolphins. **Reconciliations**: affiliative postconflict contacts between former combatants. **New affiliations**: affiliative contacts between one of the opponents and a third individual. **Spontaneous affiliations**: affiliative interactions not derived from a previous conflict.

Type of affiliation	Group 1	Group 2
New aggressions	41	14
Spontaneous aggressions	92	30
Total number of conflicts	133	44

Table 3: Total number of the different types of conflicts registered in both groups of dolphins. **New aggressions**: aggressive contacts between one of the opponents and a third individual. **Spontaneous aggressions**: aggressive interactions not derived from a previous conflict.

Tables 4, 5 and 6 shows the IA for each pair of members of the group of four dolphins. The IA registered in both groups of captive dolphins showed that affiliation was higher among same-sex members. As previously stated, the most stable and

long-lasting relationships in wild bottlenose dolphins are those between same-sex members. On the other hand, associations between females and males are, in general, weak and linked to females' reproductive state [34, 46]. Therefore, these results are consistent with the association patterns observed in the wild and in a study with captive individuals [32, 47, 48],

Dyad	Network Code	IA
Estel-Mateo	1-2	0.116
Estel-Blava	1-3	0.434
Estel-Blue	1-4	0.079
Mateo-Blava	2-3	0.050
Mateo-Blue	2-4	0.474
Blava-Blue	3-4	0.001

Table 4: Index of affiliative relationships of Group 1

Dyad	Network Code	IA
Blava-Mateo	1-2	0.000
Blava-Stella	1-3	0.533
Blava-Blue	1-4	0.000
Blava-Aitamy	1-5	0.095
Mateo-Stella	2-3	0.214
Mateo-Blue	2-4	0.525
Mateo-Aitamy	2-5	0.468
Stella-Blue	3-4	0.152
Stella-Aitamy	3-5	0.069
Blue-Aitamy	4-5	0.461

Table 5: Index of affiliative relationships of Group 2

Dyad	IA Group 1	IA Group 2	Total IA
M-M	0.474 ± 0.00	0.485 ± 0.029	0.482 ± 0.025
F-M	0.061 ± 0.042	0.088 ± 0.077	0.078 ± 0.067
F-F	0.434 ± 0.00	0.533 ± 0.00	0.483 ± 0.049

Table 6: Mean and standard deviation (SD) of the index of affiliative relationships for each possible combination of sexes in dolphin pairs. F: female, M: male.

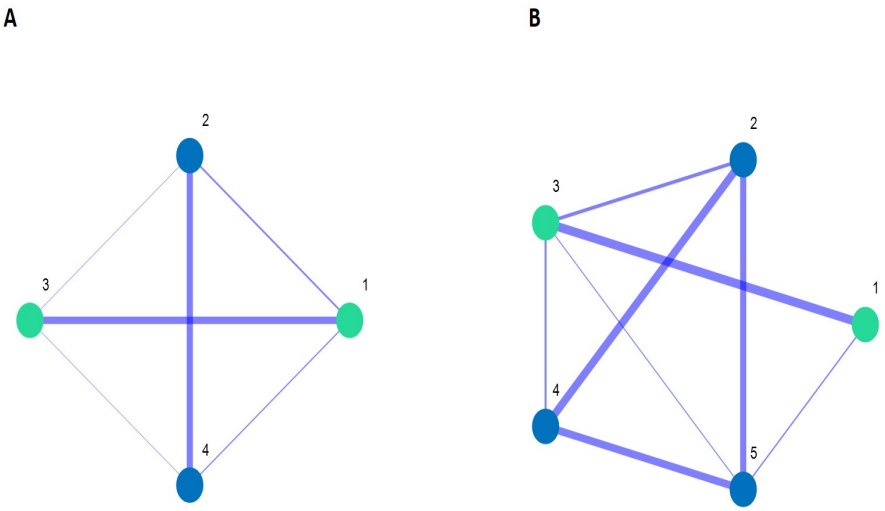

Figure 2: **A**. Weighted social networks of Group 1 and **B**. of Group 2. The width of the link represent the strength of the affiliative bond between individuals (IA). Green nodes represent females and blue ones males.

Figure 2 shows the resulting affiliative social networks of both groups of captive bottlenose dolphins. The connections between the different individuals represent the IA for each pair. The IA is a reliable measure of the affiliative bond between individuals of a social group. In both groups of dolphins the strongest bonds are the ones between individuals of the same sex. Interestingly, in the group of five dolphins the pattern of affiliative relationships is slightly different. The main differences between

the structure of both groups maybe due to the reproductive state of one of the females (Stella) in Group 2. The female was sexually receptive (trainers' personal communication) during some days of the study and thus this fact could explain why the adult males spend many time swimming synchronously with her. This is reflected in the higher IA between males and females of Group 2 (see Table 6).

The temporal social networks revealed that affiliative contacts were much more numerous than aggressive ones in both groups of dolphins (see Tables 7 and 8). The most numerous aggressive contacts in both groups were the ones between male-female pairs. In Group 1 the aggressions between male-female pairs even exceeded the number of affiliative contacts.

	Num. affiliative contacts	Num. aggressive contacts
Male - Female	318	571
Male - Male	501	30
Female - Female	486	37
Total	1305	638

Table 7: Number of affiliative and aggressive contacts of Group 1

	Num. affiliative contacts	Num. aggressive contacts
Male - Female	105	73
Male - Male	292	22
Female - Female	111	5
Total	508	100

Table 8: Number of affiliative and aggressive contacts of Group 2

Temporal and time-aggregated networks

Figure 3 shows the temporal networks of the group of four and five dolphins for one specific day. We only depicted the networks of a period that presented a change in their structure compared to the previous 3-minute period. The temporal networks for each day of the study can be found in Appendix A.

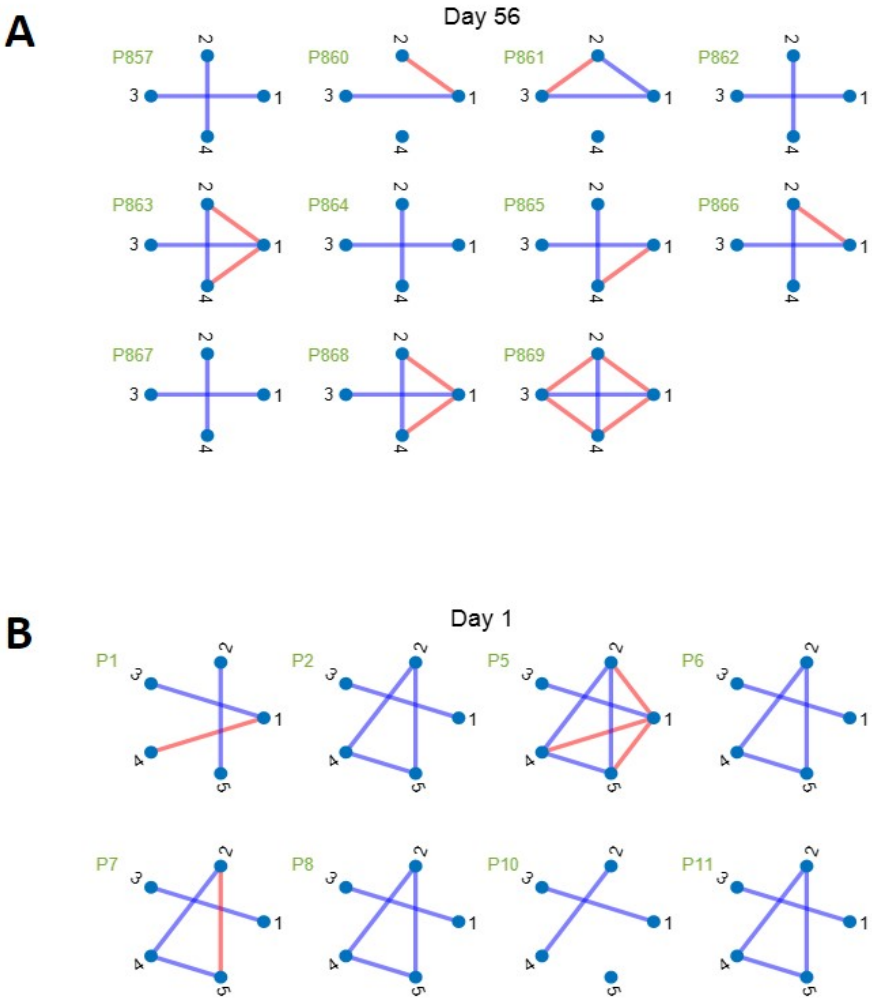

Figure 3: **A**. Temporal networks of Group 1 on day 56 and **B**. of Group 2 on day 1. P is the number of the period, red links represent aggressive interactions and blue links affiliative interactions.

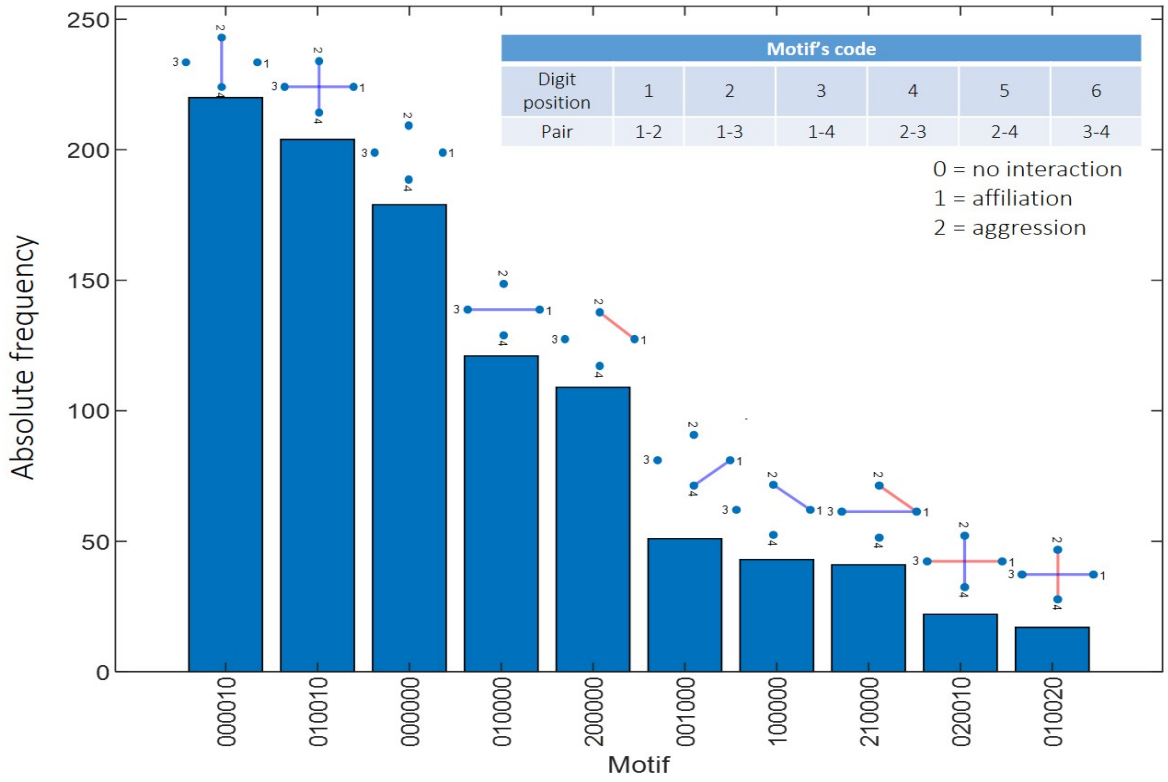

Figure 4: Most common motifs in the temporal networks of Group 1. Red links represent aggressive interactions and blue links affiliative interactions. The inset contains the motif's code: a specific digit position is assigned to each pair of dolphins. No-interactions are represented by a 0, affiliative interactions by a 1 and negative interactions by a 2.

We show the most frequent motifs for both groups of dolphins in Figures 4 and 5. In the group of four dolphins, the most common motif was the one including a positive interaction between males followed by the motif with the two possible same-sex affiliations (see Figure 4). That is, the motif in which, in the same period, both, females and males engaged in positive interactions with their same-sex partner in the group. The following was the one with no interactions followed by the affiliative motif including only interactions between females. Following these affiliative motifs

we found one including an aggressive interaction between a male (Mateo) and a female (Estel). In this motif, the other dolphins did not engage in any type of interaction. Then, we found two affiliative motifs including positive interactions between the same female (Estel) and the two males. Finally, the three last motifs include one negative and one positive interaction between pairs. In the first one, the aggression occurs between one male and a female while the other female affiliates with the one victim of aggression. On the other hand, the other two motifs include both a positive and negative interaction between same-sex pairs.

In the group of five dolphins, the most common motifs are all affiliative motifs. The first motif is the one including female-female and male-male affiliative interactions in the same period (Figure 5). Then, the motif forming a triangle between one of the females (Stella) and the two adult males. The following motif included a female-female and a male-male affiliative contact in the same period. This motif is followed by the one showing a triangle of positive contacts between the three males and the one with a triangle between one of the females (Stella) and the two adult males and an affiliation between the juvenile male and the other female. This is followed by the motif with two affiliations between same-sex pairs (the two adult females and the two adult males) followed by the one with no interactions. Finally, the two last motifs in Figure 5 correspond to, first a motif involving a positive link between the two adult males, and second a motif with a positive link between one adult male and the juvenile and another between the two females in the same 3-minute period.

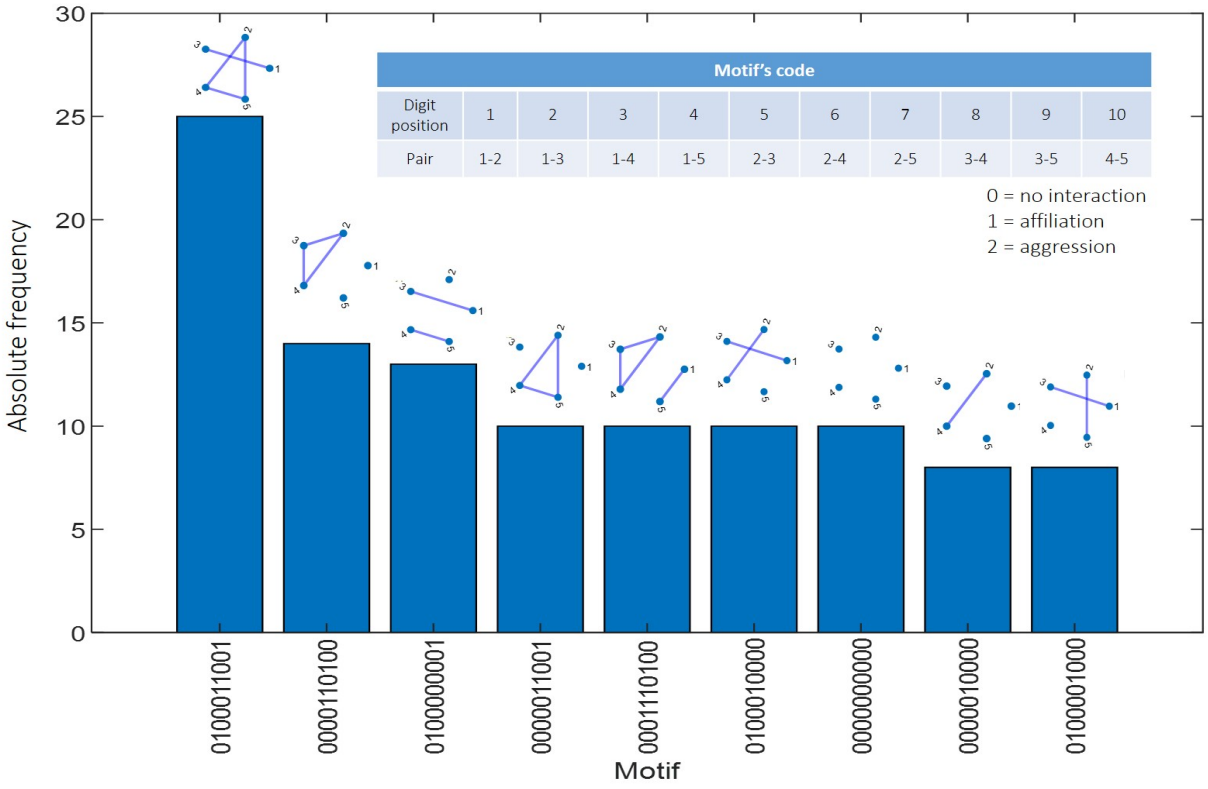

Figure 5: Most common motifs in the temporal networks of Group 2. Red links represent aggressive interactions and blue links affiliative interactions. The inset contains the motif's code: a specific digit position is assigned to each pair of dolphins. No-interactions are represented by a 0, affiliative interactions by a 1 and negative interactions by a 2.

Figure 6 shows some of the time-aggregated networks of both groups of bottlenose dolphins obtained in a specific day of recordings. The width of the link indicates the weight of the positive or negative interaction between pairs of dolphins. In general, in both groups the links presenting a greater weight were the ones of positive interactions between individuals of the same sex. Thus, in both groups, the longer affiliative interactions took place between same sex pairs for both females and males. The mean ±SD of the weight of positive links was 4.43 ±4.23 for Group 1 and 4.13 ±3.06

for Group 2. On the other hand, aggressive interactions were shorter in time as reflected by lower weights of the negative links of the time-aggregated networks in both groups. The mean ±SD of the weight of the negative links was 2.74 ±2.76 for Group 1 and 2.07 ±1.60 for Group 2. The time-aggregated networks for each day of the study for Group 1 can be found in Appendix B and for Group 2 in Appendix C.

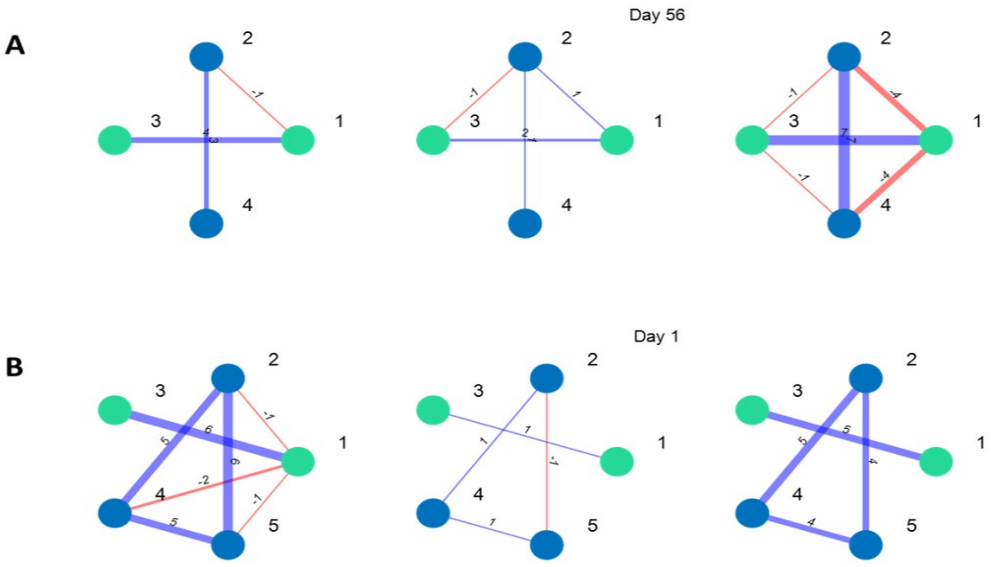

Figure 6: **A**. Time-aggregated networks of Group 1 on day 56 and **B**. of Group 2 on day 1. The number accompanying the links indicate their weight. Red links represent aggressive interactions, blue links affiliative interactions, green nodes females and blue nodes males

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Model of affiliative and aggressive interactions

Table 9 shows the probabilities of the different types of aggressive and affiliative interactions calculated for Group 1.

Figure 7 shows the number of times a specific motif appeared in the aggregated networks of the real data and in those of the two models. The number of motifs, especially in the graphs of the real data and the complex model, shows a fast decay.

Interaction	Probability per 3 minute period	Model
General Affiliation	0.1706	Simple
General Aggression	0.0718	Simple
Spontaneous Affiliation	0.0451	Complex
Spontaneous Aggression	0.0245	Complex
Reconciliation	0.0373	Complex
New Aggression	0.0072	Complex
New Affiliation	0.0128	Complex

Table 9: Probabilities per 3 minute period of affiliative and aggressive interactions in Group 1.

Thus, in these dolphins' social networks only a few specific motifs are common whereas the rest of possible motifs are scarce or absent from the networks. In turn, Figure 8 shows in more detail the normalized distribution of the twenty most common network motifs in the aggregated networks of the real data and the one of the two models. We observed that the 70 % of the 20 most common motifs of the real data were present in the simple model and 80 % in the complex model. We also calculated the Spearman's rank correlation coefficient (r_s) between the ranking of all the motifs present in the real data networks and the ranking of the motifs of each of the two models. We obtained a moderated positive correlation between the motif ranking of the real data and the one of the simple model ($r_s = 0.4083$, $p < 0.001$). On the other hand, we obtained a coefficient of $r_s = 0.7623$ ($p < 0.001$) between the real data and the complex model. That is, there was a strong positive correlation between the ranking of motifs of the real data and the ranking of the complex model.

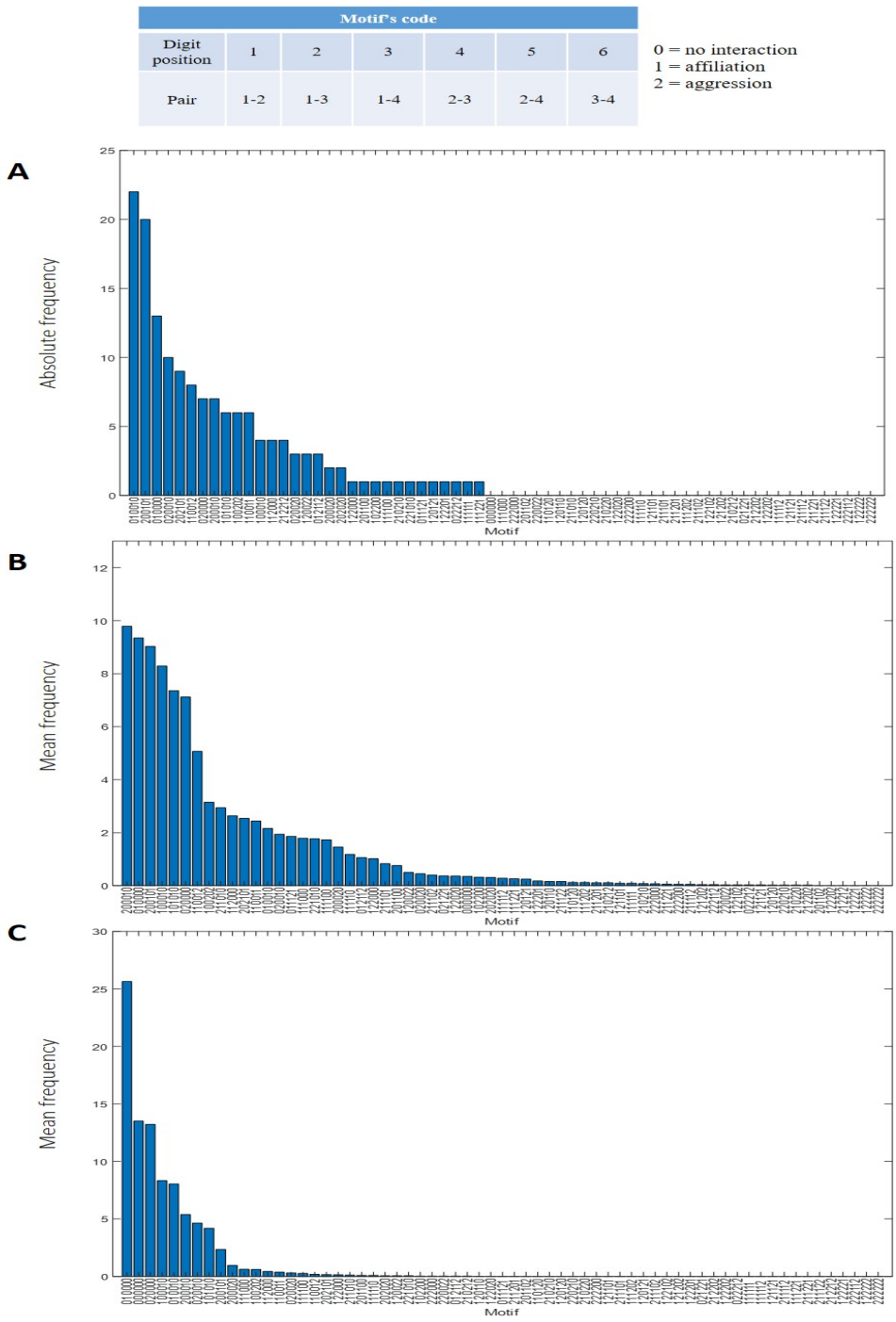

Figure 7: **A**. Frequency of the motifs of the aggregated networks of the real data, and mean frequency of the motifs of the time-aggregated networks **B**. of the simple, and **C**. complex model. The Table contains the motif's code: a specific digit position is assigned to each pair of dolphins. No-interactions are represented by a 0, affiliative interactions by a 1 and negative interactions by a 2.

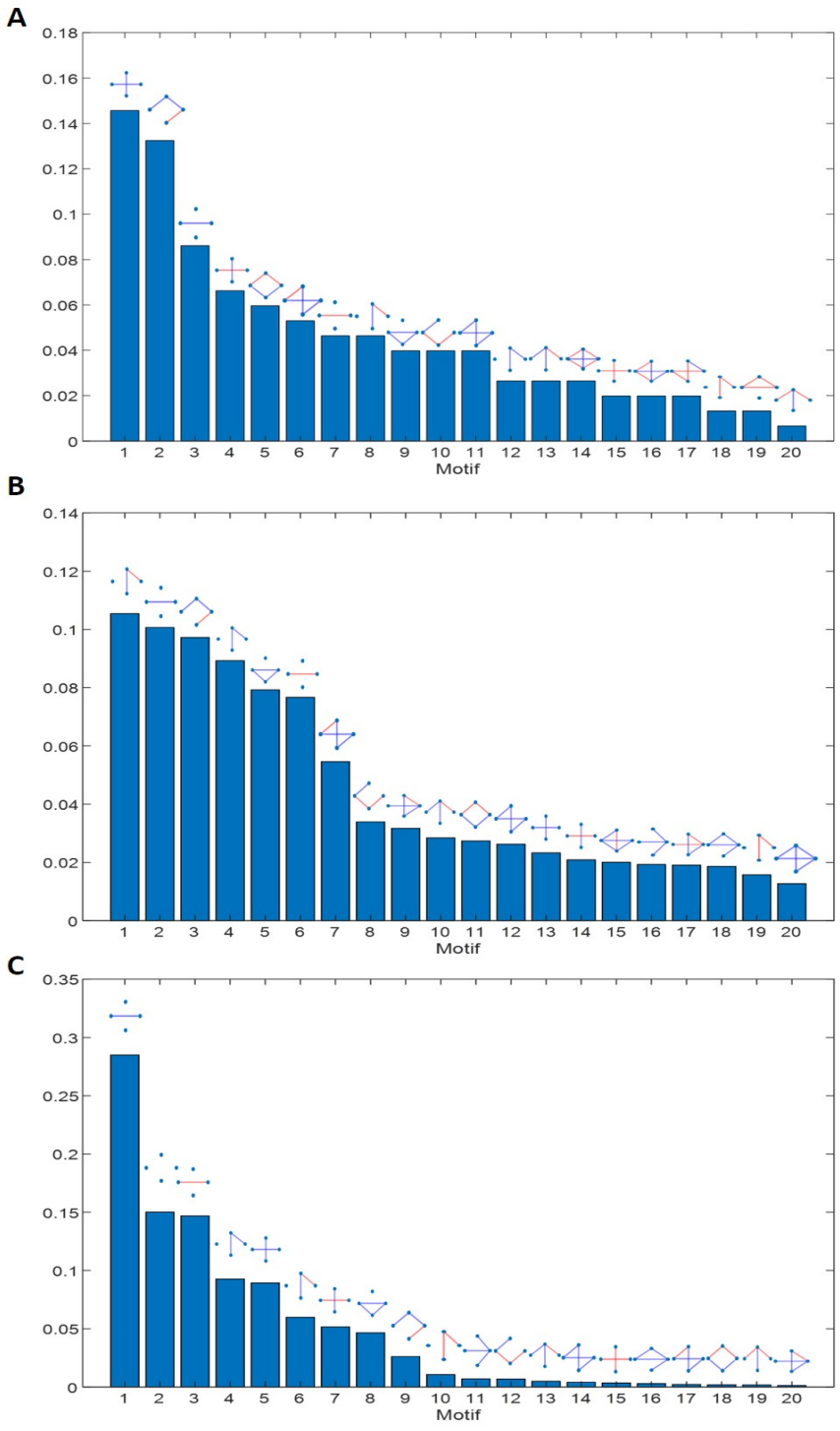

Figure 8: **A**. Normalized histogram of the twenty most common network motifs in the time-aggregated networks of the real data, **B**. of the simple model, and **C**. of the complex model. Red links represent aggressive interactions and blue links affiliative interactions.

4 Discussion

In this work, we applied some of the methods coming from the network approach to the study of the structure and features of the social networks of two groups of captive dolphins. We aimed to study the structure of affiliative and aggressive interactions in bottlenose dolphins. Finally, we also wanted to assess the presence and influence of postconflict resolution strategies in this species.

In general, data on the association levels and the social networks of both groups of captive dolphins were consistent with the association patterns observed in the wild [31, 46] and in another study with captive animals [47]. The IAs of the two groups indicated that affiliation was higher among members of the same sex compared to mixed gender pairs. Furthermore, the IAs of Group 1 were higher among males than among females. These outcomes also matched the pattern of relationships observed in wild groups of dolphins in which the most-stable bonds are those between males [46]. The results of the analysis of the most common aggressive and affiliative motifs of the temporal networks were in line with the obtained indexes of affiliation. Among the most common motifs in the temporal networks of both groups were the ones including female-female and male-male affiliative interactions in the same period.

We observed some differences between the social structure of the networks of Group 1 and Group 2. The main difference was that in Group 2 some male-female pairs presented a high IA. Furthermore, one of the most common motifs of the temporal networks of Group 2 was the one including a triangle of positive links between one of the females and the two males. This outcome is in line with the obtained IA for two of the male-female pairs of the group. As previously stated, these differences could be due to the reproductive state of one of the females of Group 2: Stella, which was sexually receptive during some of the days of the study. It has been shown that the relationships between male and female dolphins in the wild are short and

unstable in time and are influenced by the different reproductive strategies of males and females [46]. Furthermore, there are several reports of wild male dolphins with high levels of association with sexually receptive females [32, 47, 48]. Therefore, the elevated indexes of affiliation between this female and the two adult males could be a reflection of the reproductive state of Stella and the interest of the males in her during the days in which she was receptive.

The analysis of the temporal networks also indicated that, in both groups, the periods in which an affiliative contact took place were more numerous than the ones in which an aggressive contact occurred. Moreover, the time-aggregated networks revealed that affiliative contacts between dolphins often lasted several minutes whereas aggressive interactions were usually short, as reflected in the mean weight of the links of these networks. These results match the findings of other studies reporting the rate and duration of affiliative and aggressive interactions in dolphins. For example, Harvey and collaborators [47] observed that in another group of captive bottlenose dolphin the most common social behaviours were affiliative interactions among them. Furthermore, several studies have reported that, in general, dolphins present low rates of agonistic behaviour [47, 13, 36]. In addition, we found that, in both groups, the highest rate of aggression corresponded to male-female pairs. This result is in line with previous studies reporting a high rate of aggression between mixed sex pairs. [47]. It has been suggested that this high rate of agonistic behaviour between male-female dyads could be due to sexual coercion of males over females [49]. Given that in both groups females were the main receivers of the attacks from male dolphins the hypothesis of sexual coercion seems to apply to this case.

We built two models of affiliative and aggressive interactions to examine the dynamics of social behaviours in a small group of dolphins. With these models, we also aimed to assess the presence and influence of postconflict behaviours (reconciliation, new affiliations and aggressions) on the structure of dolphins' social networks. In

these two models we didn't take into account the sex or the identity of the dolphins.

The results of the simple model already captured some of the dynamics observed in the group of four dolphins. Many of the affiliative and aggressive motifs obtained with this model were also present in the networks of the real data. In addition, there was a moderate positive correlation between the motif ranking of this model and that of the real data, as reflected by the value of the r_s. In turn, the addition of the pattern of conflict resolution previously observed in the complex model improved the results of the simple model. The outcomes of the complex model predicted better than the simple one the dynamics and structure of the networks of the real data. In regard to the affiliative and aggressive motifs, 80 % of the most common motifs of the real data were also present in the networks of the complex model. Furthermore, we obtained a significant Spearman Rank correlation coefficient ($r_s = 0.7623$) when we compared the ranking of motifs of the real data and the one of the complex model. Thus, this result suggests that there is a strong positive correlation between these two rankings of motifs.

Overall, the results of the models point to the importance of postconflict strategies as a way to solve conflicts in social groups of dolphins. As reported by other studies [37, 39], bottlenose dolphins seem to display different post-conflict strategies to alleviate distress and reduce the costs of aggressive interactions. The outcomes of the models are quite good if we consider that they did not contain any information on sex, index of affiliation or the reproductive state of the animals. That is, the complex model was able to reflect very accurately the observed dynamics of this group of dolphins even though we only took into account the general probabilities of postconflict contacts. On the other hand, sex and the reproductive state seem to be crucial factors influencing the structure and dynamics of dolphins' groups. Therefore, future models should take these factors into account. In this way, an interesting starting point for future models could be to calculate the specific probabilities of engaging

in postconflict interactions for each dolphin pair based, for example, on their IA or on their gender. That is, it is likely that gender and the quality of the relationship between two dolphins affect the probability of directing aggressive or affiliative contacts to another dolphin after a conflict. In fact, it has been shown that individuals that are closely bonded to victims of aggressions tend to direct more postconflict affiliations to these individuals than other members of the group [50]. Thus, instead of selecting in each step a dolphin at random to establish or not a link between this individual and one of the former opponents, a better approach could be to select a dolphin based on its relationship with the combatants of the fight. Then, the link would be established depending on the different probabilities of displaying aggressive and affiliative contacts of that specific individual. In addition, although the complex model uses a short time memory of the last action at the time of creating the new link, it would be also a good improvement to expand this memory and consider all the previous actions.

The small sample size has been a limiting factor at the time of extracting solid conclusions on the influence of sex, affiliation index or reproductive state on the social structure of bottlenose dolphins. Therefore, future research should try to address the influence of these factors on dolphins' social structure and post-conflict strategies. For example, it would be interesting to assess the influence of the reproductive state of dolphin females on the features of the same social group. Furthermore, due to the small size of the networks we were unable to study more complex motifs like triangles, which can shed light on basic social mechanisms [27]. For example, some authors have focused on these triadic structures assessing the transitivity and structural balance of these motifs in social networks of gregarious animals such as marmots [27]. Structural balance theory predicts that some configurations of triads, especially the ones conformed by positive relationships, should be transitive (e.g. a friend of a friend is a friend) and stable in time or balanced. On the other hand, intransitive triadic

configurations, constituted by positive and negative links (e.g. an enemy is the friend of a friend), are expected to be less stable or unbalanced [27]. In general, according to this theory, social networks are expected to have more balanced than unbalanced triangle motifs [27]. There has been a long-standing interest in this theory since, the study of triads, allows to infer general local rules influencing the larger scale of the social network from a still simple motif of three nodes. However, there are only a few studies testing these predictions in social animal species.

Overall, the network approach reveals as a powerful tool to apply to the study of conflicts and social dynamics in groups of animals. Studying the main features and structure of animal social networks using models that simulate the observed dynamics can expand our knowledge on the social life of many gregarious species. Furthermore, the outcomes of these models can have applications in the management of captive groups of animals in zoos.

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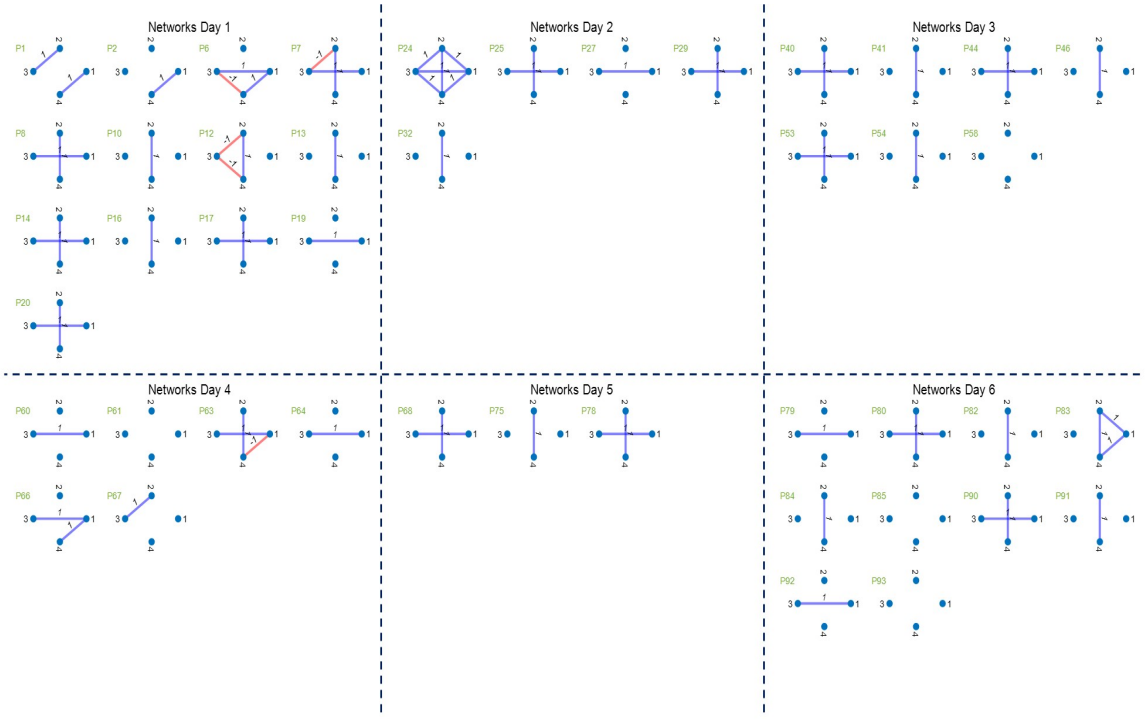
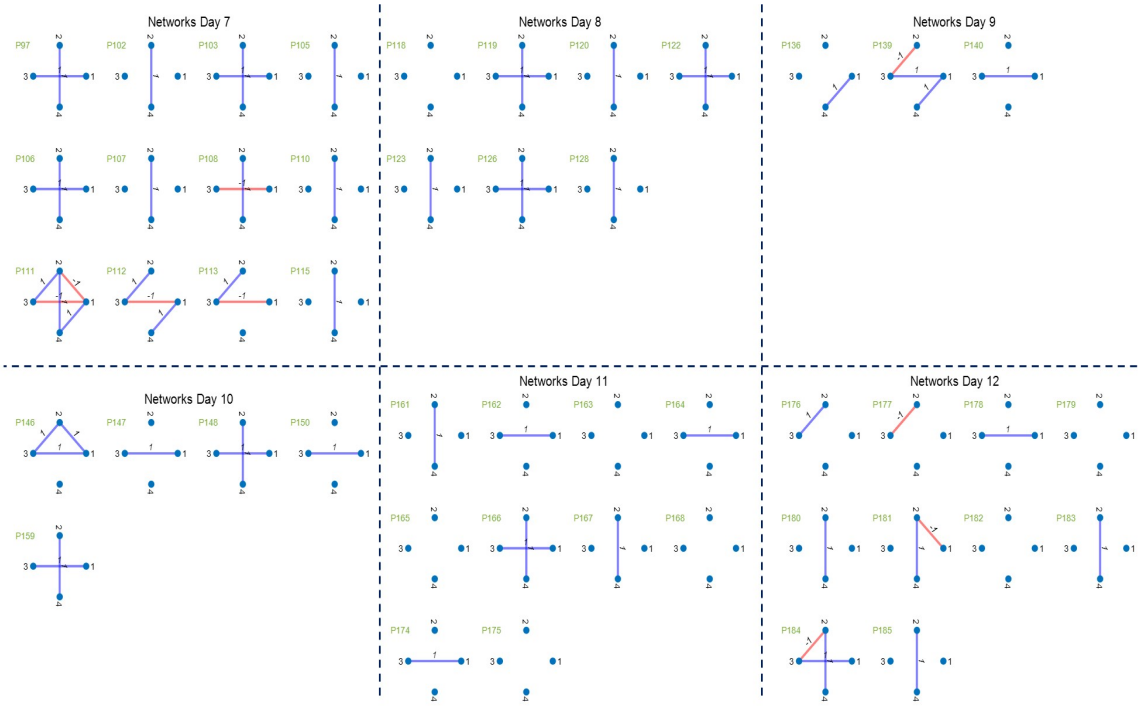
1 Appendix A: Temporal networks of the group of four dolphins

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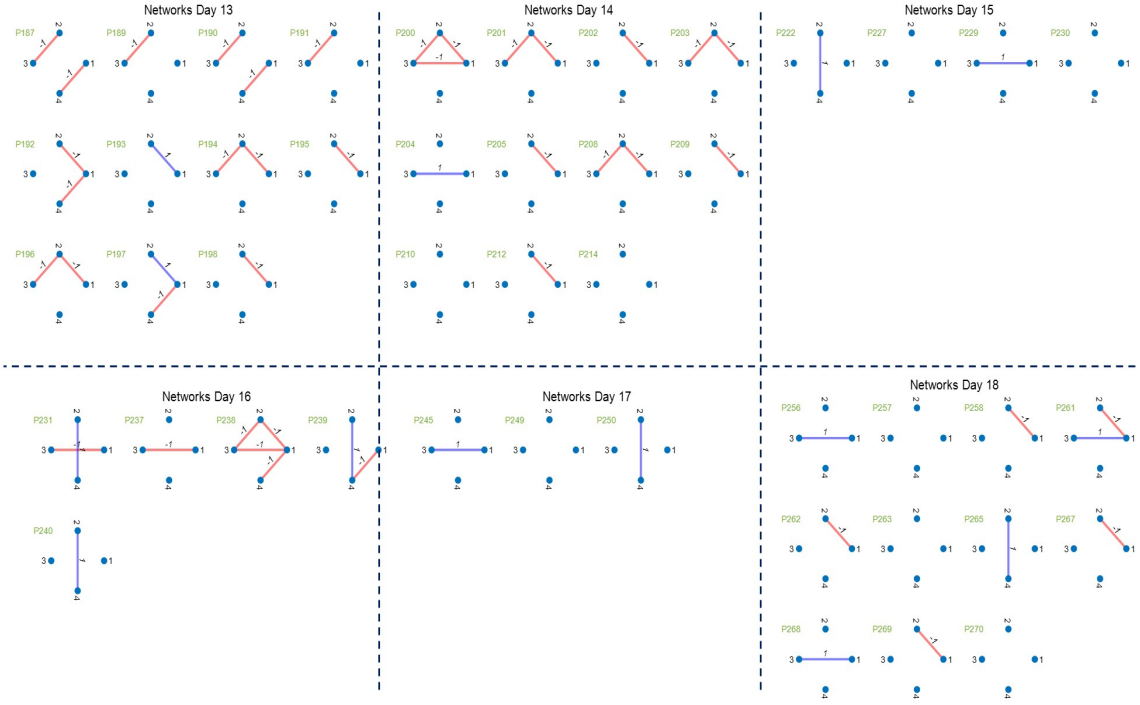
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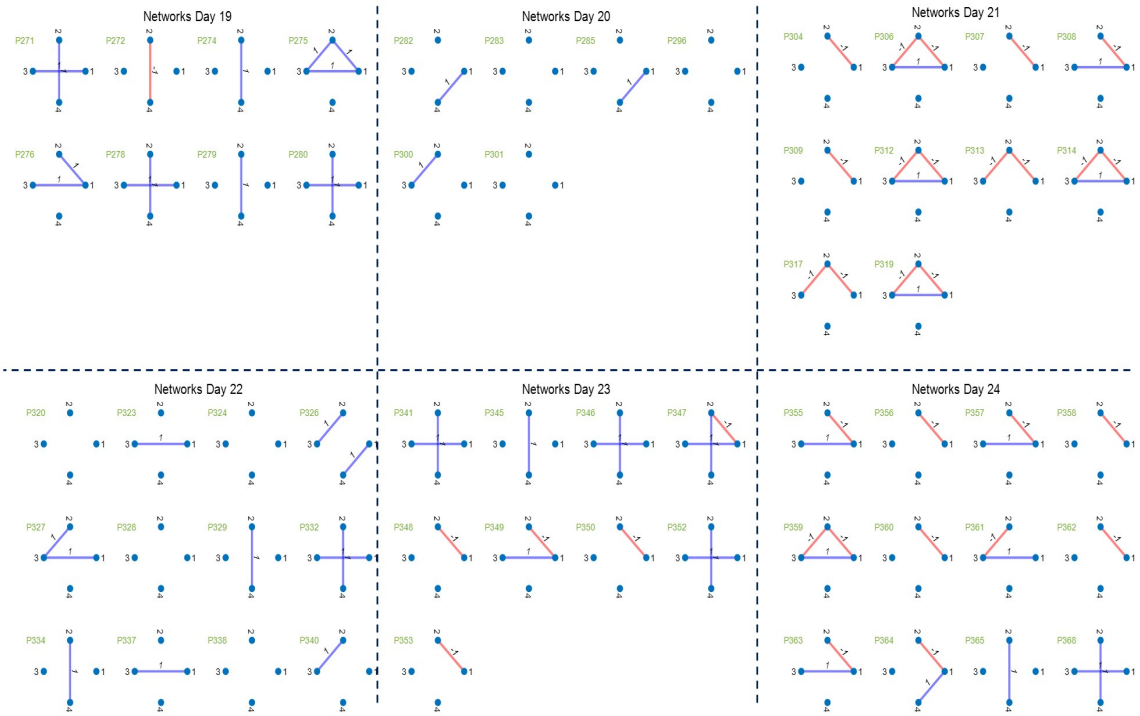
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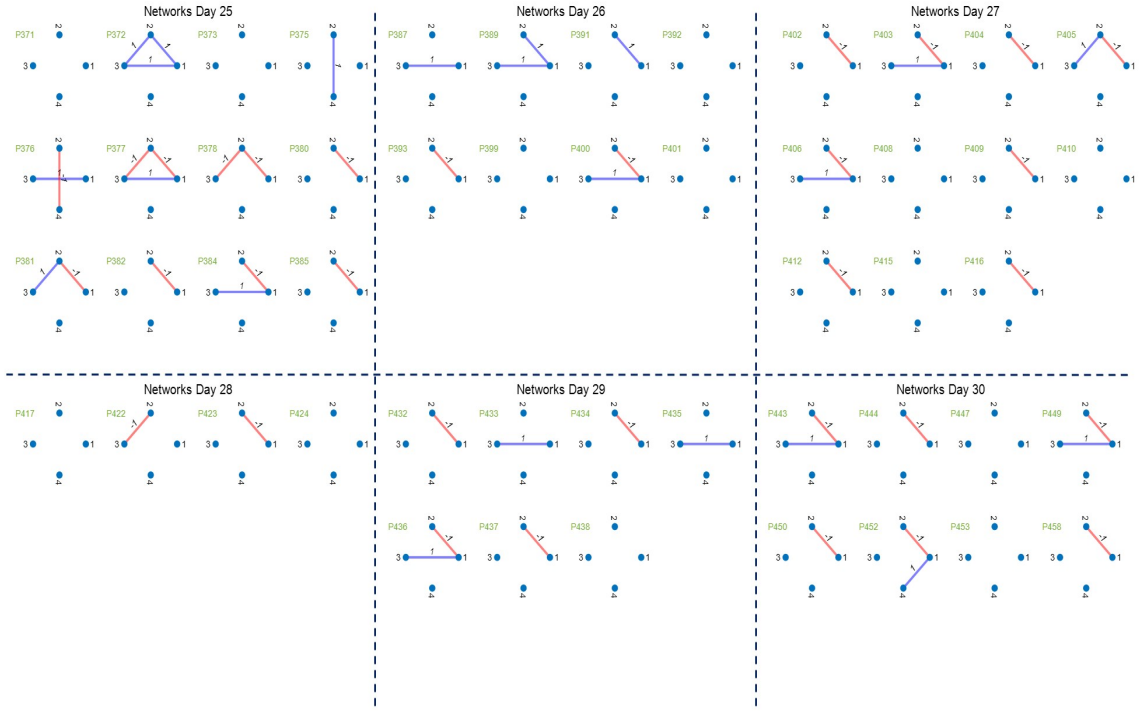
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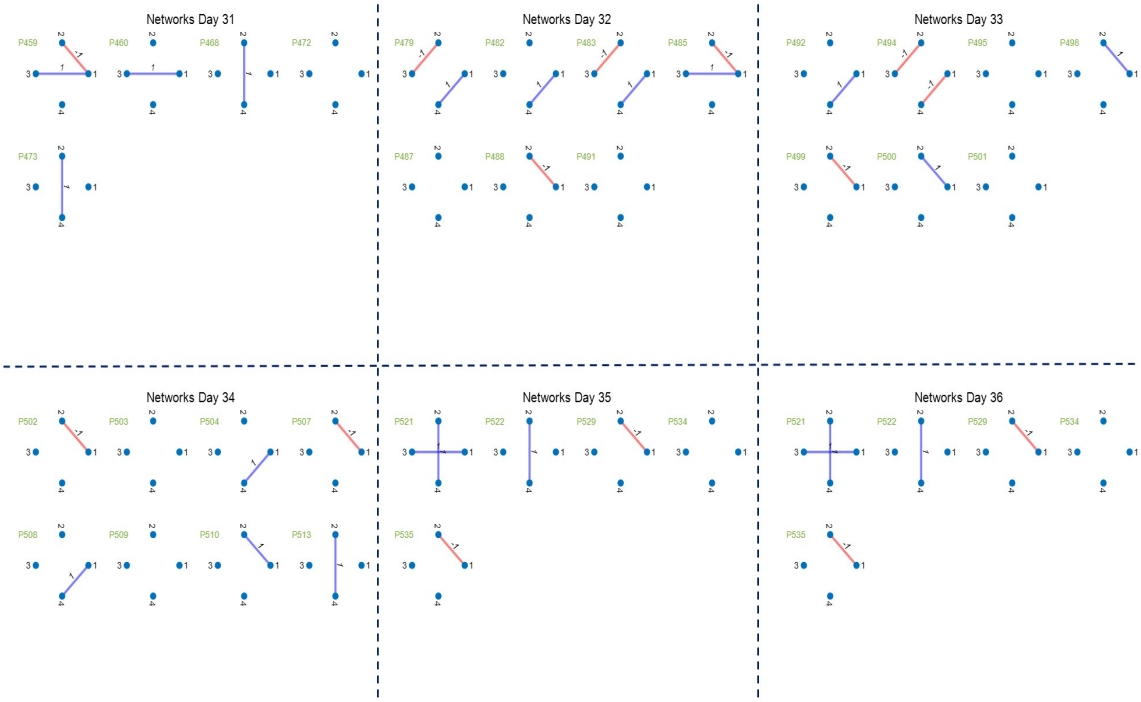
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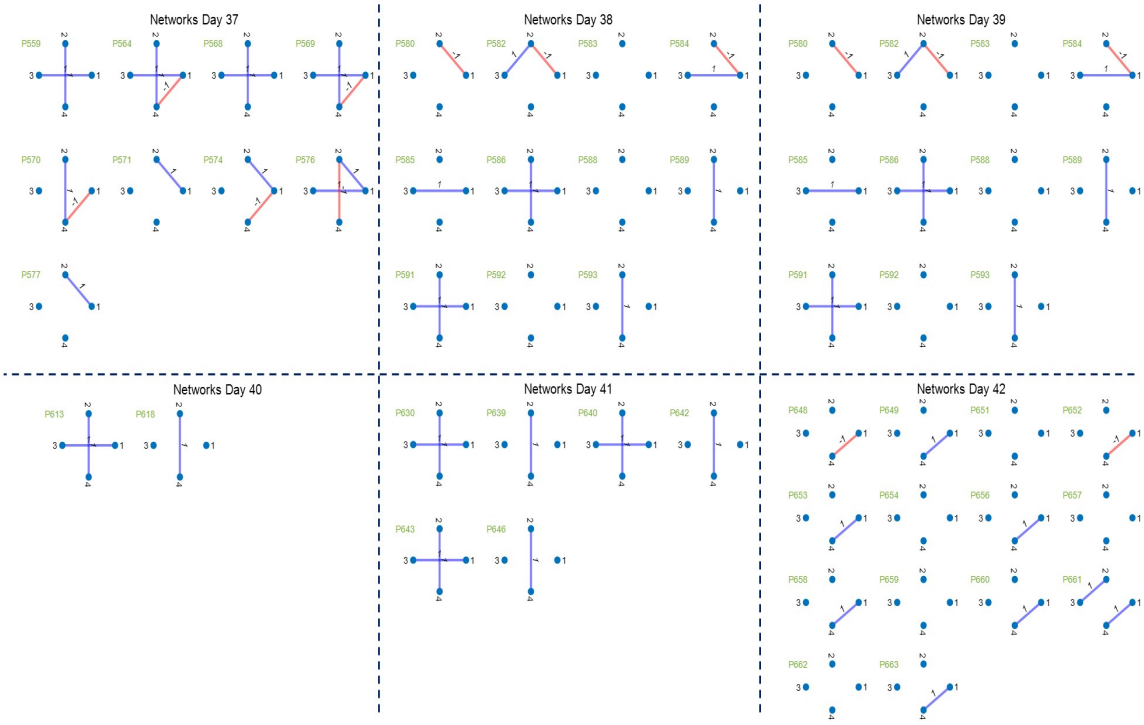
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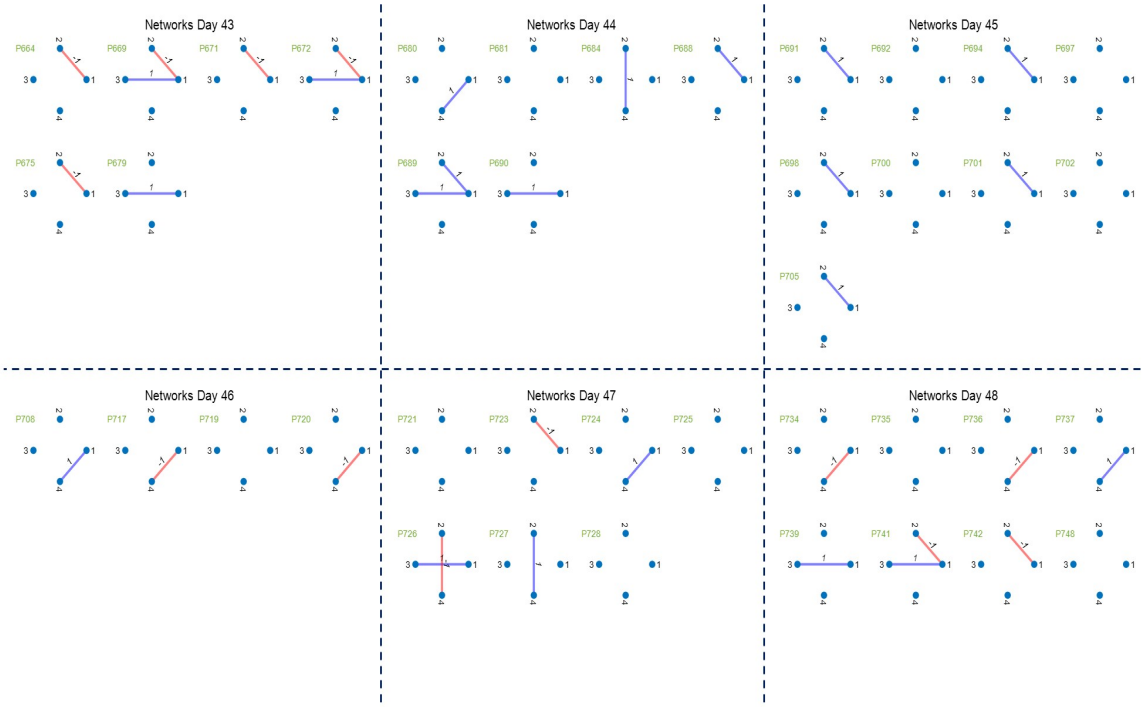
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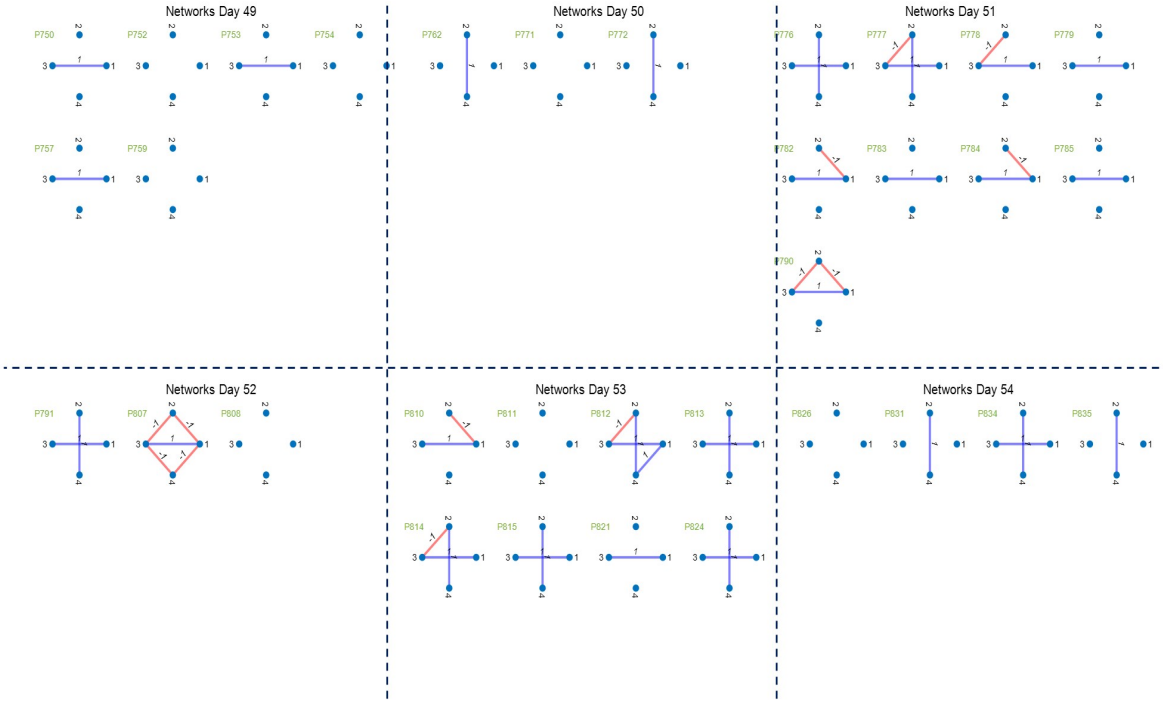
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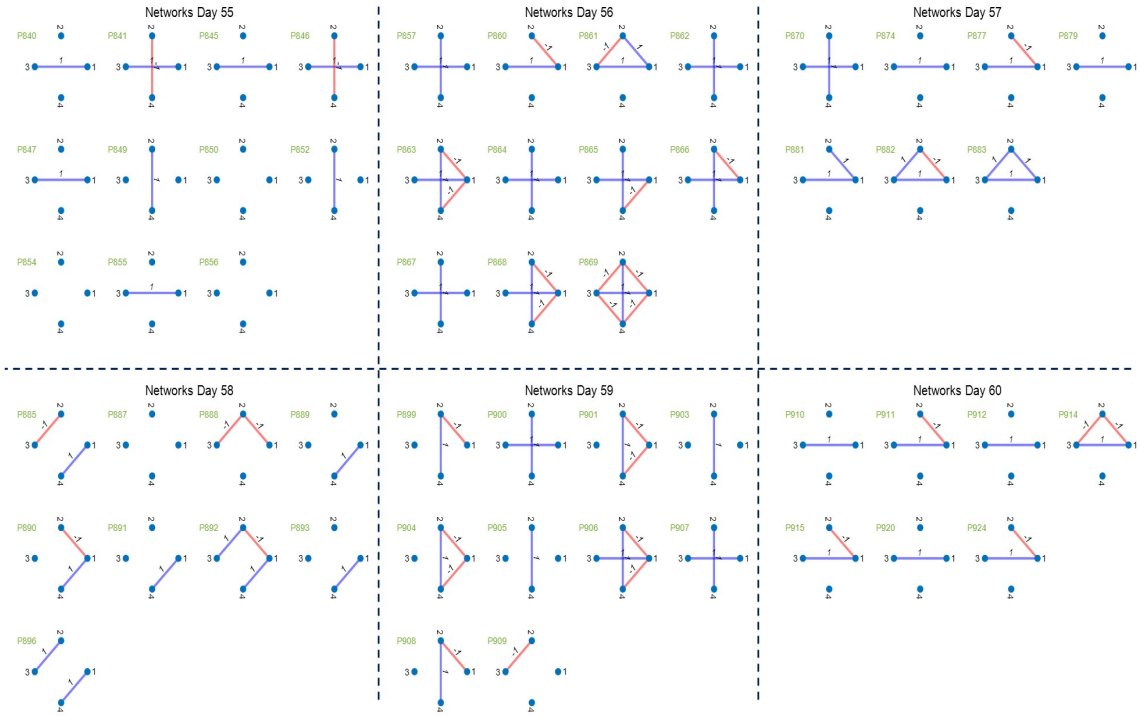
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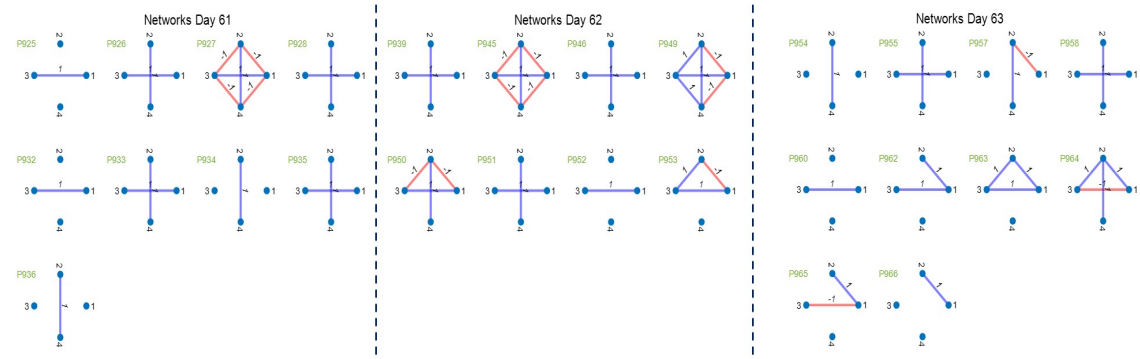
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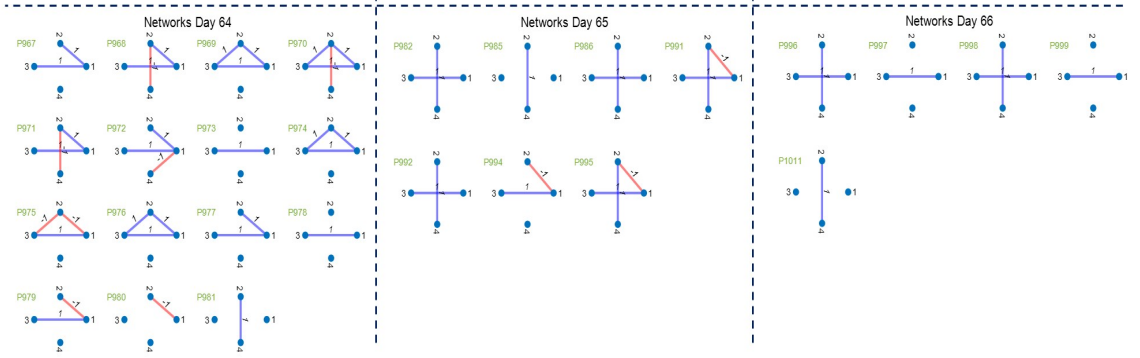
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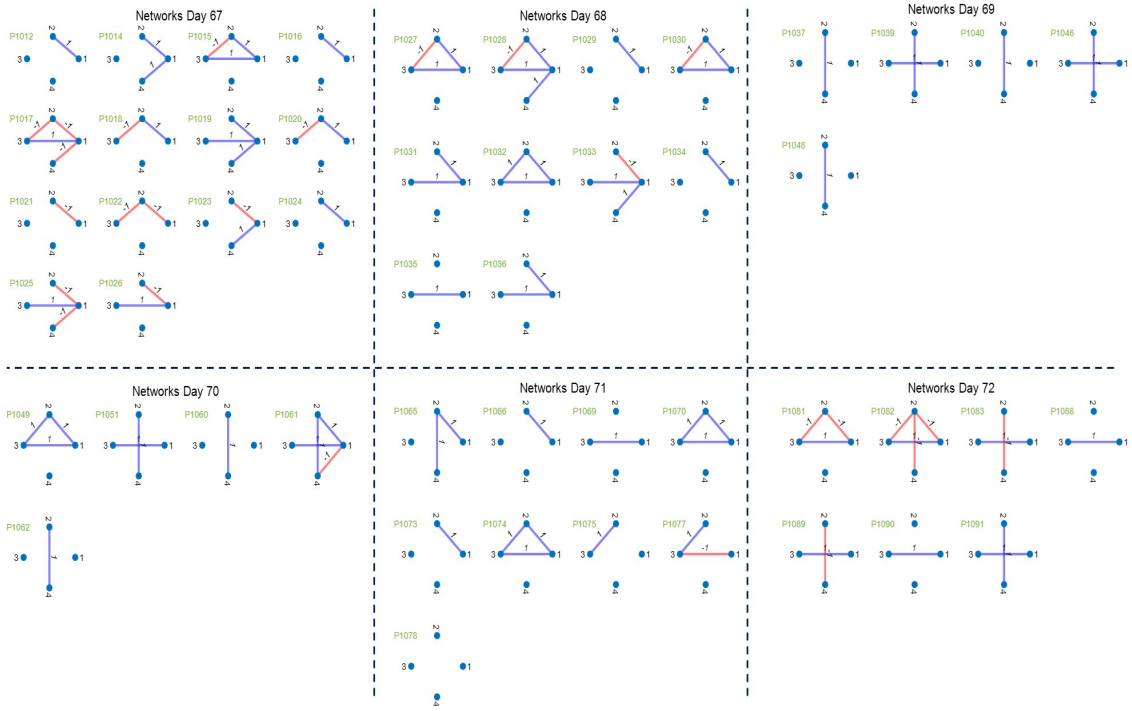
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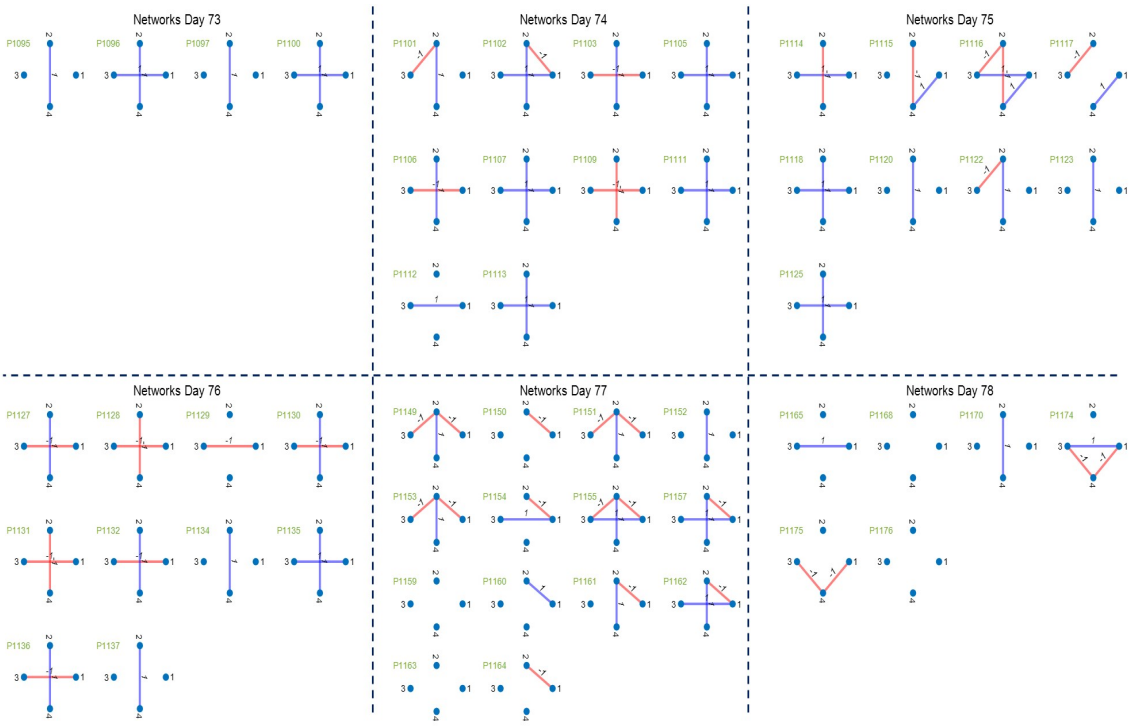
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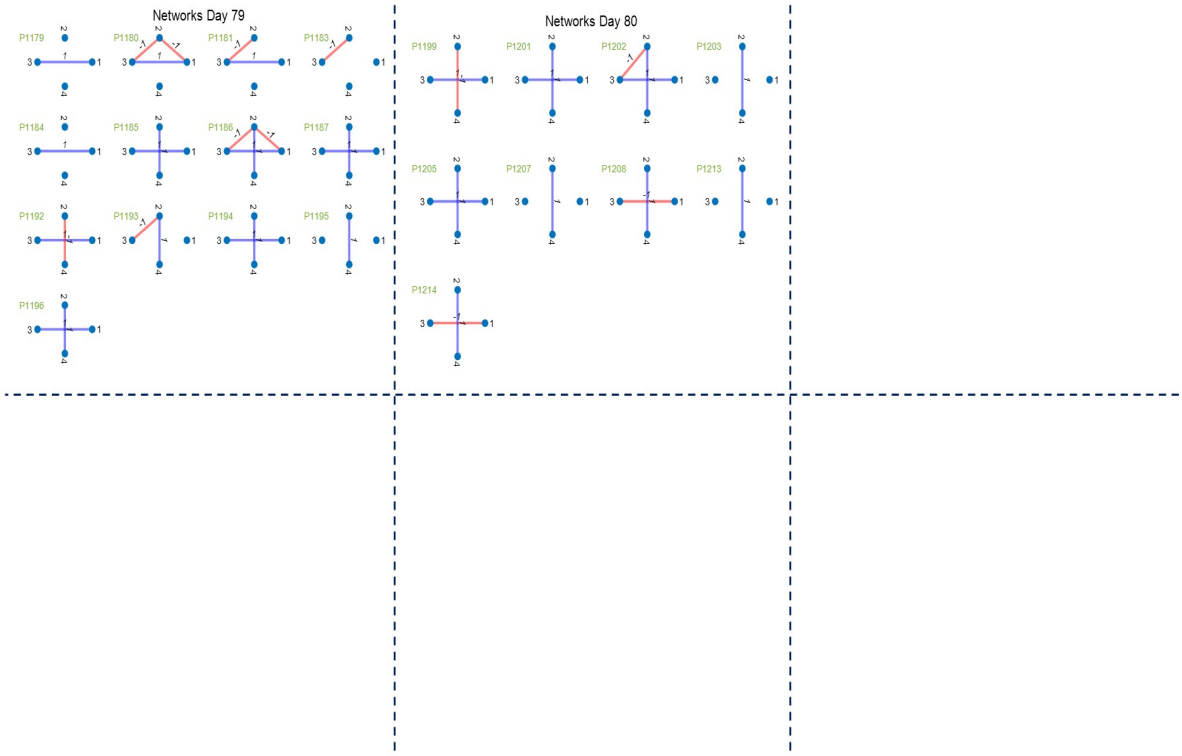
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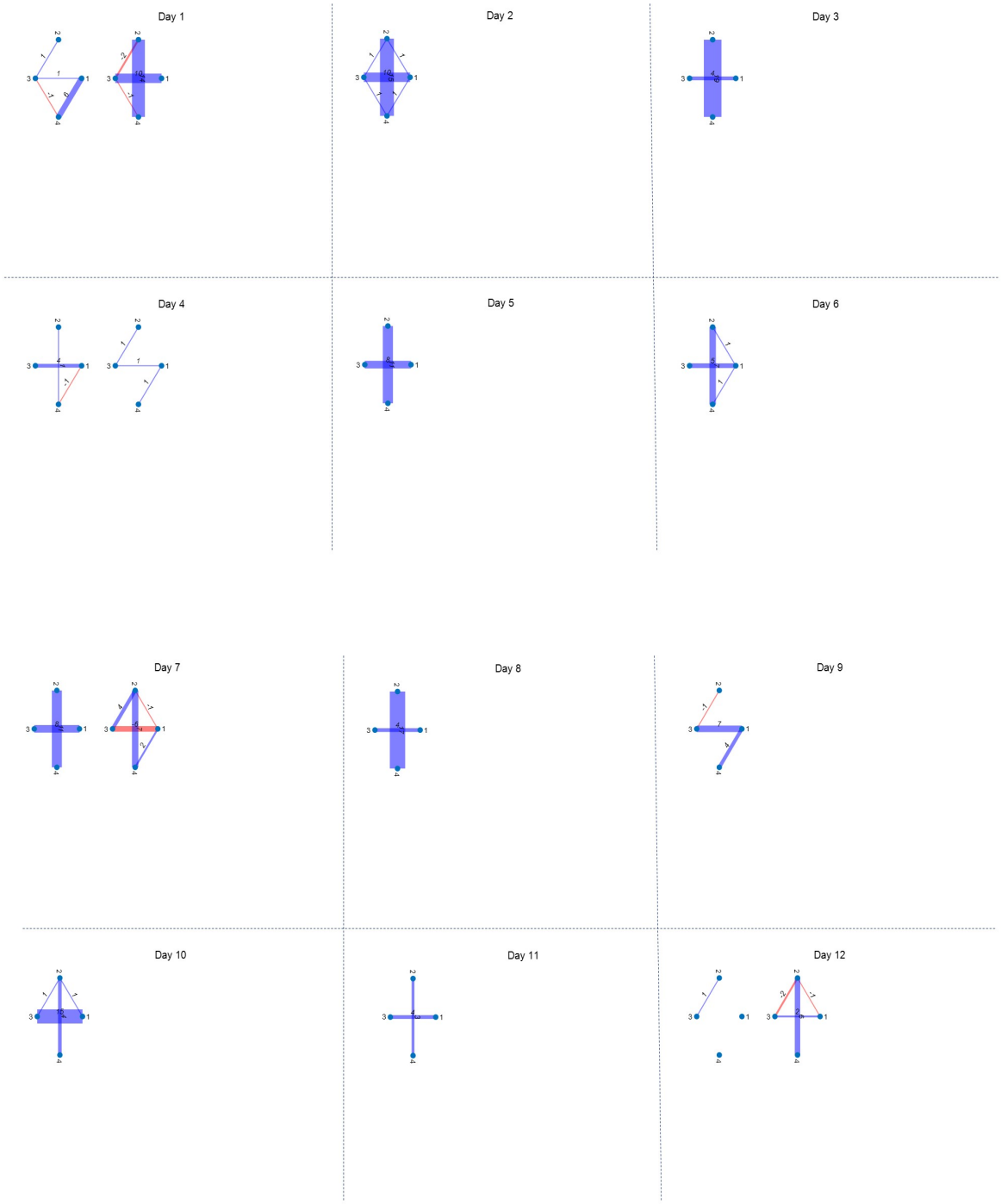
2 Appendix B: Time aggregated networks of Group 1



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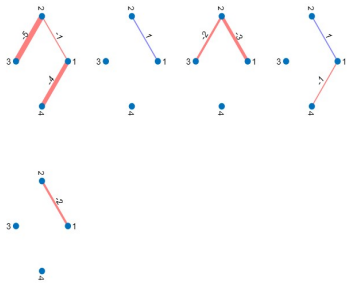

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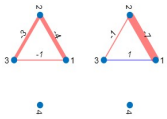

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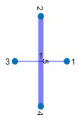

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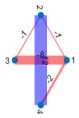

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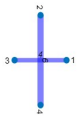

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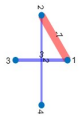

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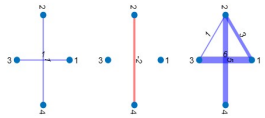

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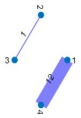

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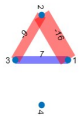

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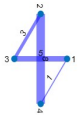

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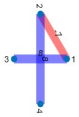

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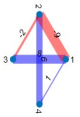

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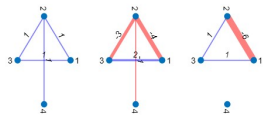

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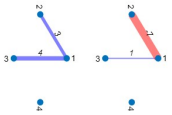

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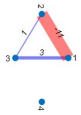

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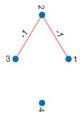

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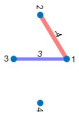

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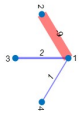

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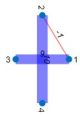

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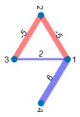

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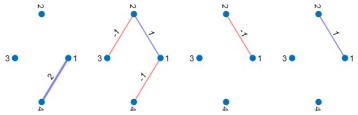

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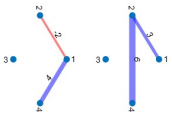

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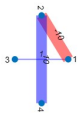

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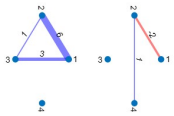

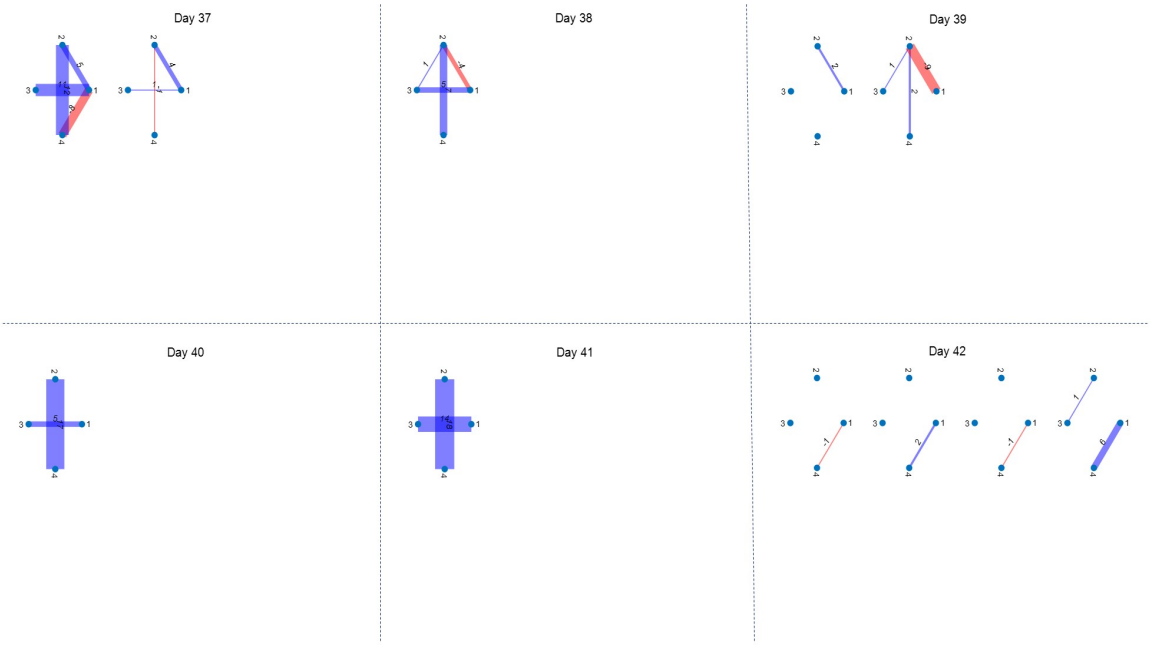
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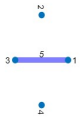

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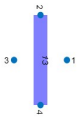

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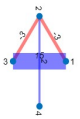

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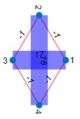

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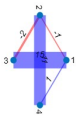

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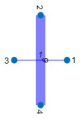

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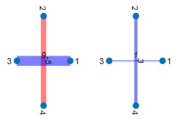

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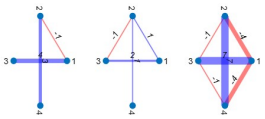

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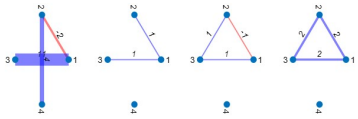

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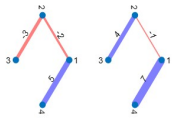

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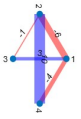

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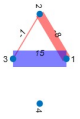

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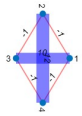

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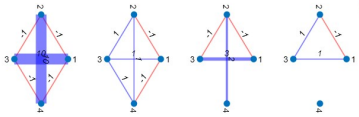

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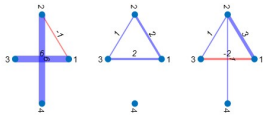

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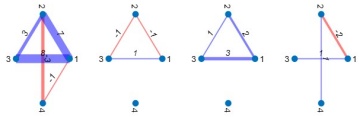

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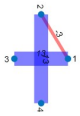

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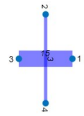

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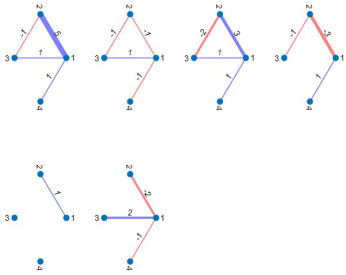

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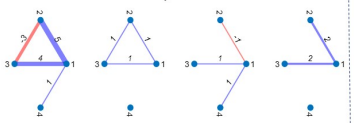

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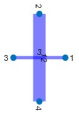

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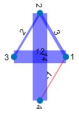

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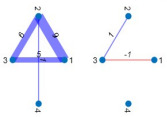

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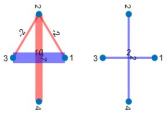
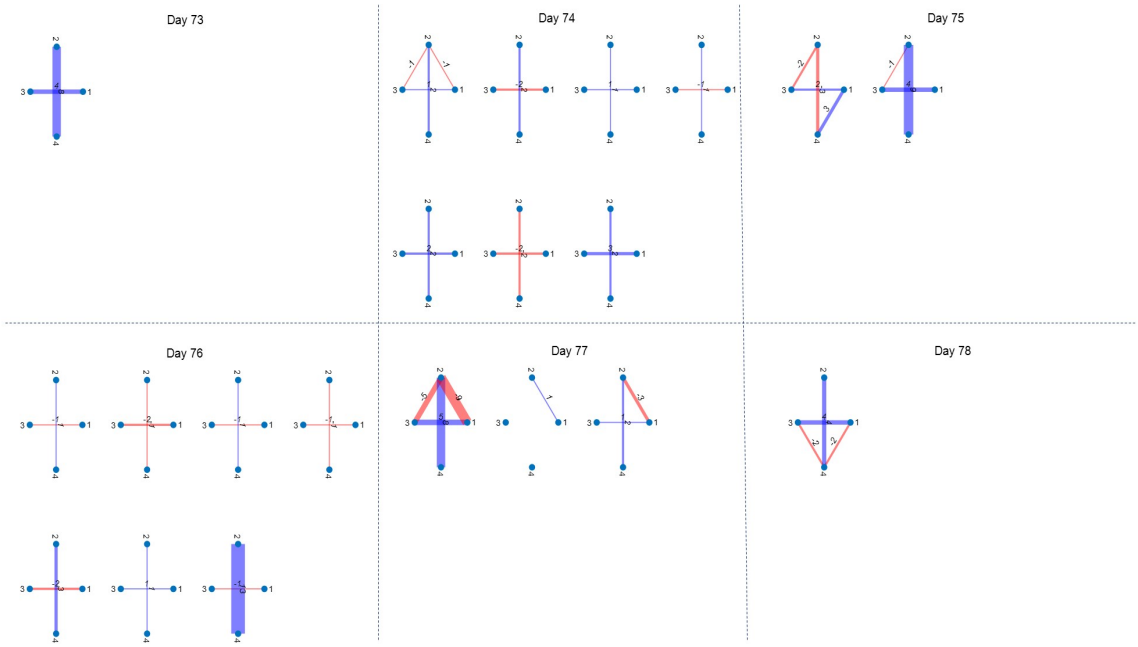
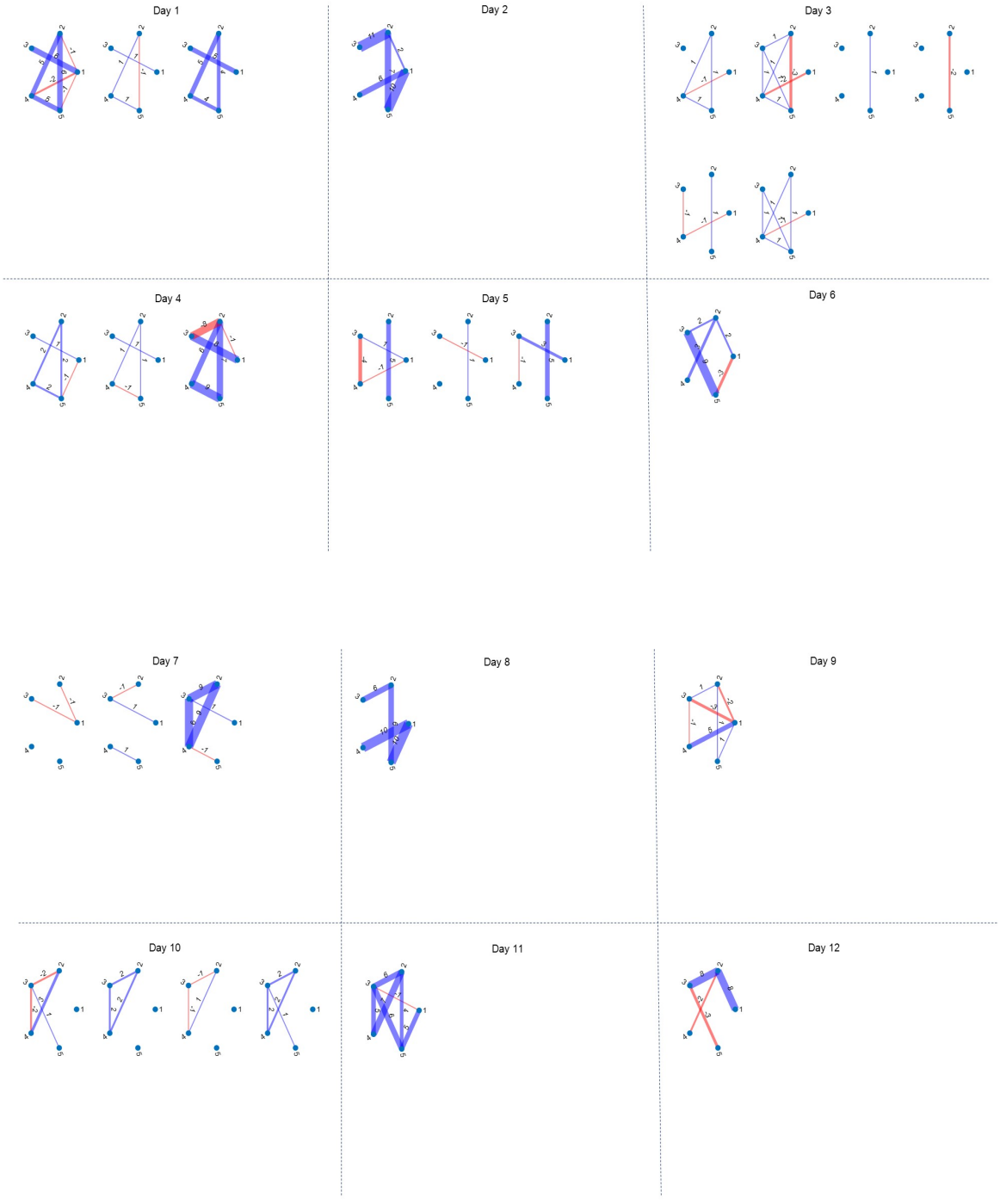



Day 73
Day 74
Day 75
Day 76
Day 77
Day 78
Day 79
Day 80

3 Appendix C: Time aggregated networks of Group 2



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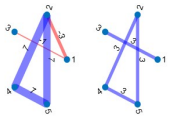

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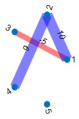

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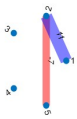

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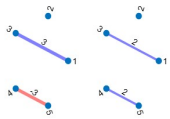

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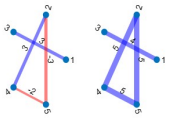

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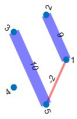

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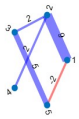

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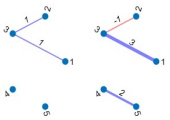

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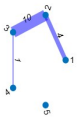

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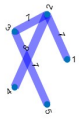

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